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COLD-WATER PREY FISH MONITORING AND ECOLOGY IN LAKE OAHE

BY

NICHOLAS B. KLUDT

A dissertation submitted in partial fulfillment of the requirements for the

Doctor of Philosophy

Major in Wildlife and Fisheries Sciences

South Dakota State University

2020

DISSERTATION ACCEPTANCE PAGE

Nicholas Kludt

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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Several additional faculty members have been instrumental in my growth as a biologist. Chris and Susan Felege, of the University of North Dakota, are signposts in my education and I appreciate everything they did for my wife and I. Some of my best memories and lessons came from Susan and Chris. Brett Goodwin, also of the University of North Dakota, provided two excellent quantitative courses that I continue to appreciate. Brad Rundquist gave me my first job in natural resources, mapping breeding bird habitat with LiDAR. The late Dr. David Willis was a constant presence at SDSU, and

for a while the American Fisheries Society universe seemed to orbit Brookings, South Dakota. His leadership built a program that was respected nationally, and it is impossible to over-state his impact on fisheries science. It is remarkable how many fisheries professionals have ties to the applied fisheries science juggernaut created by Dr. Willis and the SDSU fish faculty. I am proud and humbled to be a part of the Willis Nation legacy.

While the preceding all influenced my growth as a professional, that growth was atop a foundation laid by others. They also deserve recognition.

My friend and early teacher Ceil Anne Clement had a profound influence on my life. As a Storyteller in Residence for the North Dakota Council of the Arts and an *exceptionally* talented educator, she taught countless 5th graders the art of telling stories. She also taught us to appreciate beautiful things and write about them. It likely won't surprise her that I continue to tell fish stories, although now they are factual and my audience is somewhat different.

My family has been a great source of inspiration. John Kludt got me into the outdoors at an early age and is actually the kind of guy most young boys only think their dad is. Most of my best memories are hunting and fishing with him. Shannon Kludt pushed me to realize my potential and helped me establish a strong academic foundation early in life. She was wonderfully tolerant of all of the mud and "things" I brought *indoors* from my many adventures as a young boy in the great *outdoors*. We have endlessly laughed about the infamous "C student, my @\$@" incident, and she will

appreciate its enshrinement at the SDSU library at the terminus of my formal education. Now that life has settled down a bit, I'm looking forward to doing more with them. My siblings (Sam, Isaiah, Abbie, and Anna) have provided a great excuse to take breaks from work, watch some ball games, or go hunting out west. I wish them all the best as they continue their educations. I wish my Grandpa Kermit was able to see how my life turned out, as I think he'd have gotten a kick out of it, but I was fortunate to have excellent surrogate grandfathers in Clifford Neff, "Doc" Schindler, and Virgil Novak.

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Finally, if you are reading this, odds are pretty good that you're in fisheries at SDSU and working on the Missouri River. In that case, I suggest you check out a *tiny* WPA near Garden City for duck opener, the outlet of Poinsett for divers once the small water ices up, the E-W gravel road ditches north of Volga for wild asparagus, hang a deer stand at [44°21'31.80"N, 97°04'35.59"W] on the trails from the two apple trees, and *slowly* fish the spring walleyes near the Lake Poinsett beach or east boat ramp. The slough north of those apples, free for the picking, is good for pheasants when it freezes, and the Lake Sinai smallmouth bass generally act like largemouth bass in the SW basins. There are morel mushrooms in most woodlots on the public land south of Madison, SD. Hopefully you enjoy it all as much as I did.

CONTENTS

ABSTRACT	ix
CHAPTER 1: INTRODUCTION	1
Dissertation Content and Format	5
References	6
CHAPTER 2: A COMPARISON OF HYDROACOUSTIC SURVEY DESIGNS FOR LAKE OAHE, SOUTH DAKOTA	10
Abstract	10
Introduction.....	12
Methods	13
Results	19
Discussion	22
Management Recommendations.....	27
References	29
CHAPTER 3: DETERMING LAKE OAHE, SOUTH DAKOTA, COLD-WATER FISH POPULATION DISTRIBUTION AND HYDROACOUSTIC SURVEY COVERAGE	42
Abstract	42
Introduction.....	43
Methods	45
Discussion	49
Results	53
Management Recommendations.....	56
References	57
CHAPTER 4: RAINBOW SMELT SPAWNING POPULATION AND HABITAT CHARACTERISTICS IN A MISSOURI RIVER RESERVOIR.....	71
Abstract	71
Introduction.....	72
Methods	74

Results	80
Discussion	83
Management Recommendations.....	89
References.....	91
CHAPTER 5: EVALUATING RAINBOW SMELT LARVAL DYNAMICS IN MISSOURI RIVER RESERVOIR HABITATS	108
Abstract	108
Introduction.....	110
Methods	111
Results	116
Discussion	118
Management Recommendations.....	121
References.....	123
CHAPTER 6: A CASE HISTORY OF RAINBOW SMELT AS A RESERVOIR FORAGE FISH IN LAKE OAHE, SOUTH DAKOTA	138
Abstract	138
Introduction.....	140
Methods	142
Results	150
Discussion	153
Management Recommendations.....	159
References.....	160
CHAPTER 7: CONCLUSIONS.....	178
Research Outcomes.....	180
Research Needs	183
References.....	185

ABSTRACT

COLD-WATER PREY MONITORING AND ECOLOGY IN LAKE OAHE

NICHOLAS KLUDT

2020

In Lake Oahe, a large mainstem Missouri river reservoir that spans 375 river kilometers in central North and South Dakota, naturalized Rainbow Smelt are the primary forage species for a regionally important Walleye *Sander vitreus* fishery. Walleye condition in Lake Oahe is highly correlated to Rainbow Smelt relative abundance through time, the latter species being typified by erratic abundance trends since accidental introduction in 1971. Cisco *Coregonus artedii* were introduced in the early 1990s to augment the cold-water prey base. We evaluated Lake Oahe cold-water prey base monitoring and dynamics through: 1.) a comparison of two hydroacoustic survey designs, 2.) an evaluation of survey timing and effort for the cold-water prey base, 3.) an evaluation of Rainbow Smelt spawning ecology, 4.) an evaluation of Rainbow Smelt larval life history, and 5.) an analysis of Rainbow Smelt and Cisco recruitment dynamics with extensions to Lake Oahe Walleye. We demonstrated that an abbreviated survey technique using short, longitudinally oriented transects generated comparable data to the more time-intensive historic monitoring plan. We also documented relatively consistent estimates regardless of survey timing. The number of transects required to achieve an acceptable degree of accuracy reflected current practices. Rainbow Smelt spawning was strongly related to water temperature, consistent with observations elsewhere in their range. Steeply sloping and deeper habitats were associated with greater spawning abundance, becoming more

pronounced as spring warming proceeded. We also documented faster larval Rainbow Smelt growth at these sites, despite cooler water temperatures. Rainbow Smelt recruitment was related to heating degree days, indicating stronger year class production in earlier springs. Recruitment was also related to lower reservoir elevations, perhaps linked to greater availability of preferred adult spawning habitat. Greater Cisco recruitment was observed following Rainbow Smelt population collapses, consistent with other systems with concurrent populations. Walleye condition, historically responsive to Rainbow Smelt abundances, may have recently decoupled with the availability of alternative prey. Although beneficial to the management of Lake Oahe, the work presented here contributes to the general understanding of Rainbow Smelt and Cisco interactions and recruitment, and offers a simplified methodology for the monitoring and estimation of cold-water prey abundances.

CHAPTER 1: INTRODUCTION

Standardized monitoring is an important component of fisheries management (Bonar et al. 2009). It is used to detect interannual variation in fisheries population dynamics and make management decisions thereupon. Population dynamics are the result of variation in recruitment, individual growth, and mortality, as influenced by biotic and abiotic factors. The role of abiotic habitat on recruitment variability has been widely explored for a variety of species, with variables describing landscape-scale factors often identified as important (e.g. temperature, Hansen et al. 2015). Site-scale habitat variables such as substrate (Gosch et al. 2006), reservoir elevation (Felts 2018), and flow (Maceina and Bettoli 1998) can also be influential, and act in conjunction with landscape-scale factors. Biotic factors such as intra- or interspecific relationships are usually of secondary importance, yet can be dominant recruitment drivers in certain instances (e.g. Ricker 1975).

Recruitment of a species found in diverse habitats can be influenced by a diversity of factors. In the Atlantic Northeast, Rainbow Smelt *Osmerus mordax* are native to both inland lakes and estuarine systems. In the Great Lakes, naturalized Rainbow Smelt inhabit similar systems. Rainbow Smelt also have been introduced to large Missouri River reservoirs, as well as canyon reservoirs in the American West. Recruitment drivers differ across systems, which might be expected given the different landscape context and spatial scales of systems.

In Lake Oahe, a mainstem Missouri river reservoir spanning 375 river kilometers in central North and South Dakota, Rainbow Smelt are the primary forage species for a

regionally important Walleye *Sander vitreus* fishery (Fincel et al. 2014). Walleye condition in Lake Oahe is highly correlated to Rainbow Smelt relative abundance through time (Felts 2018, Graeb et al. 2008), the latter species being typified by erratic abundance trends since accidental introduction in 1971 (Graeb et al. 2008, Lott et al. 2001, Johnson et al. 1995). Cisco *Coregonus artedii* were introduced in the early 1990s to augment the unstable cold-water prey base (Johnson et al. 1995), and remained at low relative abundances until 2012. The factors affecting recruitment of these two cold-water prey species are poorly understood in Lake Oahe.

The need for cold-water prey fish monitoring paralleled the introduction and development of a salmonid fishery in the stratified lower third of Lake Oahe, located in central South Dakota. This fishery focused on Chinook Salmon *Oncorhynchus tshawytscha*, and the Rainbow Smelt – Walleye linkage was already known while this was being developed. Early cold-water prey monitoring relied on passive gears. From 1985-2000, suspended gill nets were deployed annually at 3 sites across the reservoir (Johnson et al. 1995, Lott et al. 2001). As pelagic species, Rainbow Smelt and Cisco were heterogeneously distributed across the reservoir. This led to concerns about prey base estimate reliability from a small number of netting stations (Lott et al. 2001). To achieve greater spatial survey coverage and to increase confidence in the cold-water prey base estimate, hydroacoustic monitoring was used intermittently starting in 1983 (Burczynski et al. 1987, Nelson-Statsny 2001) and was adopted as an annual survey in 2000 through the present (Fincel et al. 2016). Hydroacoustic methods evolved through time as new equipment was purchased and new analysis methods developed, with 3 time periods

corresponding to gears. The heterogeneous distribution of the cold-water prey base remains a challenge for survey design.

Rainbow Smelt and Cisco have been widely surveyed with hydroacoustics, and the acoustic properties of the Rainbow Smelt population in Lake Oahe (Burczynski et al. 1987, Fincel et al. 2016) and elsewhere (Parker-Stetter et al. 2006) are well-documented. Vertical beaming surveys are generally conducted at night due to the photosensitivity of Rainbow Smelt (Appenzeller and Leggett 1995). Additionally, vertical migration leads to changes in aspect as the fish moves up or down in the water column, which can have an effect on acoustic return signal strength (Appenzeller and Leggett 1992). Surveys are generally composed of discrete transects, or continuous scans covering a whole waterbody (Gangl and Whaley 2004, Taylor et al. 2005) or region thereof (Parker-Stetter et al. 2006). In the case of Lake Oahe, surveys are composed of discrete transects (Fincel et al. 2016). It would be beneficial to clarify the pros and cons of different types of transect, survey timing, and survey effort, as this would enable more efficient use of South Dakota Game, Fish and Parks resources.

The heterogeneous distribution of Rainbow Smelt in the reservoir, and the challenges this has historically posed for monitoring, may reflect spatial habitat patterns. Summer distribution of the zooplanktivorous fish may be the result of reservoir productivity gradients. In the stratified lower end of Lake Oahe, reservoir productivity follows a gradient from mesotrophic in the northernmost stratified reaches to oligotrophic near the dam (Fincel 2011). The more oligotrophic southern reaches are typically assumed to support lower abundances of Rainbow Smelt. Likewise, spring

warming patterns may influence spawning site selection, with more spawning occurring in those areas that warm more quickly (Winemiller and Rose 1991). Such reservoir-scale patterns have been anecdotally described but never quantified in Lake Oahe.

Finally, Rainbow Smelt larval dynamics may vary according to local habitat conditions (e.g. O'Brien et al. 2012). Adult site selection plays a major role in the growth and survival of larval fish. This is a linked process, with greater size equating to greater survival (Michaletz 2010). Larval fish are therefore highly vulnerable to both benefits and costs associated with rearing habitat quality (Hjordt 1926, Houde 2008). Spawning and rearing habitat management is therefore known to be important, but this management is complicated in reservoirs by the aging process. Reservoir aging is accelerated relative to natural lakes because reservoirs are often engineered for maximum water capture, thus accelerating the geomorphic processes of sedimentation and eutrophication (Wetzel 2001, Miranda and Krogman 2015). These processes are associated with the degradation of aquatic habitats and are directly or indirectly the focus of large-scale reservoir restoration projects (Pegg et al. 2015). Natal and rearing habitats therefore may be threatened or degraded prior to being understood.

To evaluate monitoring designs and survey logistics considerations, to investigate Rainbow Smelt spawning site use and resultant larval life history, and to broadly understand the recruitment dynamics of Lake Oahe Rainbow Smelt and Cisco populations and their relationship with the sport fishery, I developed the following five objectives: 1.) a comparison of two hydroacoustic survey designs and survey timing, 2.) an evaluation population distribution and varying levels of sampling effort for

estimation of the cold-water prey base, 3.) a description of Rainbow Smelt spawning ecology, 4.) a description of Rainbow Smelt larval life history, and 5.) an analysis of Rainbow Smelt and Cisco recruitment dynamics with extensions to Lake Oahe Walleye.

Dissertation Content and Format

In addition to the introductory and conclusion chapters, this dissertation contains 5 research chapters, presented sequentially following the preceding objectives. As each chapter is written as stand-alone research paper, some redundancy within methods sections is inevitable. I use the pronoun “we” to reflect the collaborative nature of the work presented here. As I expect to publish with coauthors, this pronoun usage respects their contributions. However, I assume responsibility for the content and conclusions of the research chapters in this volume. All chapters are formatted following the American Fisheries Society style guide.

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CHAPTER 2: A COMPARISON OF HYDROACOUSTIC SURVEY DESIGNS FOR LAKE OAHE, SOUTH DAKOTA

Abstract

Rainbow Smelt *Osmerus mordax* and Cisco *Coregonus artedii* are the primary coldwater forage species in Lake Oahe, South Dakota. Understanding the population dynamics of these species is an important aspect of Walleye *Sander vitreus* and Chinook Salmon *Oncorhynchus tshawytscha* management, the two dominant sportfish species in Lake Oahe. As these coldwater species are pelagic and heterogeneously distributed throughout the stratified reservoir zone, they have been historically surveyed using hydroacoustics. Hydroacoustics offers the ability to efficiently survey large areas but can be resource and time consuming. We compared the traditional cross-sectional transects (2.5 ± 0.8 km, $n = 17$) with an abbreviated longitudinal transect (0.5 ± 0.0 km, $n = 17$) survey, using a paired design replicated over three months and two years ($n = 97$). We then compared observed target densities of Rainbow Smelt and Cisco using a mean square error (MSE) approach. Observed densities were highly correlated for both Rainbow Smelt ($r = 0.91$) and Cisco ($r = 0.94$). Decomposing MSE revealed random error components of 67.3% and 99.7% of Rainbow Smelt and Cisco, respectively, indicating no systemic differences between the paired estimates. We also examined if insignificant differences in estimates would be magnified by data expansion. We estimated relative abundance using inverse distance weighted interpolation, and compared results using MSE. In addition to survey method, ANOVAs of mean relative abundance by month and year were not significant for either Rainbow Smelt ($p = 0.61$) or Cisco ($p = 0.96$). The

longitudinal transect survey time was 60.99% faster, and generated comparable data.

We therefore recommend the adoption of the 17 abbreviated longitudinal transects for future standardized sampling of Lake Oahe coldwater stocks, with flexibility regarding future standard sampling month choice dependent on agency workloads.

Introduction

Inland fisheries management is dependent on the ability to manage predator-prey relationships. Knowledge of prey abundance trends enables managers to forecast potential changes throughout trophic levels in the fishery and adjust management accordingly (Noble 1981). Although passive gears were historically common for surveying some cold water prey fish stocks, active gears such as hydroacoustics have now been widely adopted (Simmonds and MacLennan 2005).

Over the past 30 years, new technologies, survey designs, and estimation methods have been explored for mobile hydroacoustic surveys as agencies developed their hydroacoustic protocols for standard monitoring programs. Mobile hydroacoustic sampling provides large-scale survey coverage in a relatively short time, reducing the effects of fish movement and behavior on population estimates (Simmonds and MacLennan 2005). Thus, mobile hydroacoustic sampling has seen widespread implementation for monitoring cold water prey species in 2-tiered fisheries (e.g. Beuchamp et al. 1997, Gangl and Whaley 2004, Fincel et al. 2016).

Rainbow Smelt *Osmerus mordax* are the primary cold water prey fish in Lake Oahe, South Dakota, a major main-stem reservoir on the Missouri River, and are annually surveyed using hydroacoustics. We sought to provide recommendations for a new survey protocol by 1) comparing density estimates generated from two transect types, a full reservoir cross section and a shorter longitudinal transect, 2) examining the differences in survey duration between transect type, and 3) evaluating the potential consequences of surveying later in the summer. We hoped to demonstrate a less time-

intensive survey could yield similar results, thereby increasing crew safety by reducing the duration of night work on a large reservoir with unpredictable weather, with the additional benefit of survey cost savings.

Methods

Study area – Lake Oahe is the second largest storage reservoir on the Missouri River, stretching 372 km from central North Dakota to central South Dakota (Figure 2.1). At normal pool, Lake Oahe's surface area measures 145,000 ha. The upper portion of Lake Oahe in South Dakota is mesotrophic, and transitions to oligotrophic downstream toward the dam (Fincel 2011). The reservoir stratifies during the summer months, with the northern extent of stratification typically occurring just upstream of the Moreau River tributary arm (River Mile 1177, Burczynski et al. 1987, SDGFP, unpublished data). Additionally, the Cheyenne River tributary arm shallows in its western extent, and the stratified zone within this region varies by year and month. Cold water species are thereby constrained to the lower 169 km of Lake Oahe, which has an approximate area of 68,500 ha (Figure 2.1).

Hydroacoustic surveys – Mobile hydroacoustic sampling is commonly used to estimate the abundance or biomass of pelagic species (Parker-Stetter et al. 2006, Simmonds and MacLennan 2005). A hydroacoustic system emits sonar pings, which propagate through the water column, and, upon contact with a fish, return an echo to the survey unit. The ratio of returned to emitted energy for a single fish, referred to as target strength (TS), then is converted to length via TS – fish length formulas.

Since the mid-1980's, hydroacoustic sampling has been conducted on Lake Oahe by South Dakota Department of Game, Fish, and Parks (SDGFP). A standardized nighttime survey was completed annually in July since 2000. In 2015, due to equipment upgrades and a desire for more uniform survey coverage, a systematic survey was adopted. The new survey was repeated in July, August, and September from 2015-2018 to evaluate the effects of survey timing. Additionally, two transect types were paired and examined for differences in predicted density during summers 2015-2016. The overall survey goal was to provide an annual relative abundance estimate of Lake Oahe cold water prey and to visualize general spatial distributions within the reservoir.

Because Rainbow Smelt undergo diel vertical migrations (Argyle 1982, Burczynski et al. 1987), all hydroacoustic surveys commenced 30 minutes after sundown to avoid under-estimation biases from assessing the population during the vertical movement (Appenzeller and Leggett 1992). During the day, Rainbow Smelt tend to be concentrated near the bottom of the reservoir. After dusk, they move upward in the water column to feed, and are more evenly dispersed through the water column at night, easing analysis by allowing better individual fish discrimination (Burczynski et al. 1987). Multiple nights were required to complete each survey period. We ran the surveys during the waning lunar third quarter to the waxing lunar first quarter to avoid potential for ambient light levels to affect fish behavior (Appenzeller and Leggett 1995). Although ambient light was more of a potential concern in July, when the thermocline was shallower, we continued this practice in the latter months for consistency. For the same reason, all surveys were run with vessel lights off, with the exception of required navigational lights.

Hydroacoustic surveys were conducted using a Biosonics DT-X system with a 420 kHz split beam transducer set up for vertical beaming. The transducer had a 6.9° circular beam angle, and was mounted to the side of the survey vessel on an adjustable arm. Survey settings were 5 pings/s with a pulse duration of 0.5 ms. System calibration was periodically checked according to the manufacturer's instructions using a 17.5 mm tungsten carbide target sphere and the apparatus described by Foote et al. (1987). Data were analyzed using the single echo detection biomass option with 40-log(R) time varied gain within Sonar5-Pro (Balk et al. 2015), due to low overall pelagic target densities. We excluded a 0.5 m layer immediately above the lake bed to eliminate bottom interference (Parker Stetter et al. 2006, Simmonds and MacLennan 2005). To convert TS to approximate fish length and subsequently assign a species identification, we used the TS equation from Love (1977):

$$TS = 19.4 * \log_{10}(TL) - 0.9 * \log_{10}(f) - 62$$

where TS is the target strength of an individual fish, TL is the total length (cm) of the fish, and f is the frequency of the sonar pulse in kilohertz.

Using the previous equation, we assigned individuals' TS values to species based on length frequencies from targeted deep water gill netting conducted 2012-2018, following Fincel et al. (2016). This is the concurrent sampling technique employed by SDGFP to determine species composition of acoustic targets. Rainbow Smelt and Cisco were vertically constrained by temperature during the sampling period, which coincided with annual lake stratification. Species assignment of acoustic targets was therefore limited to targets below or within the mesothermal layer. Within Sonar5-Pro, the

sampled area (ha) was determined, and fish density was quantified (fish/ha) for extrapolation beyond the immediate hydroacoustic transect.

Sampling Design Comparison – We compared two hydroacoustic transect types in 2015-2016 to determine differences in survey duration and/or sampling data generated, with our goal being maximized survey efficiency. We consider a survey to be efficient if it yields accurate density estimates with less effort (person-hours). Unfortunately, accuracy in methods comparisons can only be determined when sampling a known population (Bodine et al. 2013). Thus, we were limited to comparing transects to each other using a mean square error test, while assessing the time required to complete each design. As each transect was a discrete spatial unit and the survey was not a continuously scanned route, we elected to use the whole transect as our unit of inference, as opposed to subdividing individual transects into elementary sampling distance units.

Historically, Lake Oahe was surveyed with cross-sectional hydroacoustic transects. Cross-sectional transects were oriented perpendicular to the shore and span the entire width of the reservoir, excluding shallow littoral areas (< 3 m depth, Burczynski et al. 1987). In our design, cross-sectional transects were spaced every 11.3 km in a systematic design ($n = 17$), covering the stratified reservoir zone (Figure 2.1). At each site where cross-sectional transects were taken, we paired a 0.8 km longitudinal transect ($n = 17$) that bisected the cross-sectional transect and was oriented down the long axis of the historic Missouri River channel, now the remnant channel on the reservoir bottom. This was our best approximation of the pelagic zone, and represented

the area of maximum reservoir depth for each transect location. Our design would have yielded 102 paired acoustic samples from 17 sites surveyed over two years with three surveys per year; however, in four instances, one or both transects of a pair were not completed due to adverse weather, resulting in a reduced sample size of $n = 98$ paired acoustic transect densities.

We assessed survey efficiency by comparing the scanning time and the target densities generated by each transect type. Transect lengths were calculated using the feature geometry tool in ArcMap 10.4 (ESRI 2016). Time to complete a given hydroacoustic transect was measured using a stopwatch. Mean transect scanning time between the two designs was compared using a two-sample t-test ($\alpha = 0.05$). Fish density estimates were initially compared with a Pearson's r correlation test. Sources of error between transect density observations were assessed using a mean square error (MSE) test, which is based on a least-squares regression fitted to observed and predicted values. In our case, the regression was fitted to the paired observations from the two transect designs. The MSE represents variance from a 1:1 line, which in turn represents the two transects producing the same results. MSE can be decomposed to 3 components, where differences in the mean component (Z) are due to differences between paired values, the slope component (S) represents deviation error from unity (1:1 fit), and the residual component (R) represents random error (Rice and Cochran 1984), incorporating the correction of the original equation from Ranney (2008). We evaluated systemic errors (Z, S) between the transect designs using Bonferroni joint confidence intervals on the least squares regression which tested the joint hypothesis

that regression parameters had a 0-intercept and a slope of 1 ($\alpha = 0.05$). The MSE was repeated for Rainbow Smelt and Cisco density estimates to test for systematic differences between the transect designs.

Interpolation Methods – The basic challenge of prey fish management is maintenance of adequate stock size and structure to support predator populations (Noble 1981), which requires some method of estimating abundance or biomass of prey fish in a system. Our goal was to estimate the relative abundance of Rainbow Smelt and Cisco in Lake Oahe. We therefore needed to expand the transect density estimates to the entire reservoir.

We used a spatial interpolation technique for data expansion, using transect centroids as our input location for transect density. Inverse distance weighted (IDW) interpolation, a deterministic method (Li et al. 2018), was used to interpolate densities from both transect designs, as we were curious if small differences in local density would be magnified post-data expansion. Predictions were again compared using the MSE test. Due to small sample size if the species' abundance estimates were tested independently ($n = 6$), we included the abundance estimates for Rainbow Smelt and Cisco in a single analysis ($n = 12$). We used the pooled approach because we were assessing departure from a 1:1 line.

Inverse distance weighting functions on the premise of Tobler's First Law of Geography, "everything is related to everything else, but near things are more related than distant things" (Tobler 1970). The IDW formula is expressed:

$$\hat{Z} = \sum_{i=1}^n \frac{1}{(d_i)^p} Z_i \bigg/ \sum_{i=1}^n \frac{1}{(d_i)^p}$$

where \hat{z} the estimated value for the prediction point, z_i is the measured value of the sample point, d_i is the Euclidean distance between the sample point and prediction point, n represents the number of sample points and p is a power parameter (Li et al. 2018). The method is considered deterministic because the influence of a sample point on a prediction location is based on the intervening distance, as opposed to a model-based approach. Analyses were conducted in R using the gstat package with the default smoothing power factor $p = 2$ (R Core Team 2018, Pebesma 2004). A distance threshold was applied (11.3 km), limiting the influence of sampling points on the between-transect interpolation to the values of the upstream and downstream transect.

Finally, SDGFP has conducted an annual hydroacoustic survey in July since 2000. Because of anecdotal perceptions of relatively high July severe weather frequency, there was interest in potentially moving the survey to a later month. We therefore investigated temporal differences in July, August, and September estimates of Rainbow Smelt and Cisco from 2015-2018. We used an analysis of variance (ANOVA) with a Tukey's HSD post-hoc test to examine differences in mean density between months.

Results

Gillnetting data consistently revealed Rainbow Smelt and Cisco length-frequencies were distinct. Additionally, other species in these length ranges are rarely encountered in the hypolimnetic layer of Lake Oahe (Fincel et al. 2016, Burczynski et al. 1987). Pooled catches from 2012-2018 demonstrated the temporal stability of the pelagic prey size distributions (Figure 2.2). While there was overlap between small adult Rainbow Smelt (72%) and age-1 Cisco (28%) within the 100 mm size bin, Rainbow Smelt

were the only species within the 110 – 180 mm size bins. We therefore assumed acoustic targets 100-180 mm, proportionally corrected for the 100 bin, were Rainbow Smelt \geq age-1. Cisco dominated the 70-90 mm size bins, with the descending limb of the size distribution in the 100 mm bin. Cisco also dominated catches 190-330 mm. Although some larger Rainbow Smelt were captured (200-220 mm), their overall percentage of the catch in those bins was $\leq 0.002\%$. Acoustic targets in the upper size bins were therefore all designated Cisco, proportionally where necessary in the 70-100 mm range. In both cases, the sum of the targets within the appropriate length bins was the species density estimate at that transect.

Paired Rainbow Smelt and Cisco density estimates between the two transect designs were correlated ($r = 0.79$, $r = 0.83$, respectively). Linear regressions relating estimates for both species were significant ($p < 0.0001$). The linear models did highlight some dispersion of paired estimates (Figures 2.3, 2.4). This was lower for the Rainbow Smelt model ($\text{adj.}r^2 = 0.62$) than the Cisco ($\text{adj.}r^2 = 0.68$). For both species, the MSE test on the paired transect densities rejected the null hypothesis that the joint Bonferroni adjusted 95% confidence intervals contained an intercept of 0 and a slope of 1 (Table 2.1). This indicated a departure from the 1:1 line. The MSE decomposition of variance about the 1:1 line showed most variance was residual, representing random error (Table 2.1). The mean component was smallest, indicating low differences between the paired density estimates. The slope variance component for Rainbow Smelt was 30%, and Cisco 37%. The slope component represents deviation from the 1:1 fit. Longitudinal transects tended to generate higher density values for Rainbow Smelt (381.49 ± 240.55 , $\bar{x} \pm$

st.dev.) than the cross section transects (319.73 ± 176.76). Cisco results were similar with longitudinal transects tending to generate higher densities (313.83 ± 252.54) than cross sections (271.24 ± 196.36). Both transect designs exhibited similar magnitudes of variance, thus indicating similar gear precision. Rainbow Smelt estimates had coefficients of variation of the mean ($\frac{st.err.}{\bar{x}}$, CV) for the cross section and longitudinal transects of 0.055 and 0.063 respectively. Similarly, Cisco CVs for the cross section and longitudinal designs were 0.073 and 0.081, respectively. Although cross sectional transects were more precise for Rainbow Smelt and Cisco, overall precision for both methods was excellent. Thus, the longitudinal transects were judged to generate higher densities with similar precision.

The MSE on the IDW interpolation density estimates failed to reject the null hypothesis that the joint Bonferroni adjusted 95% confidence intervals contained an intercept of 0 and a slope of 1 (Table 2.2). Although not statistically significant, in practical application the abundance estimates derived from the longitudinal transects were $13.65\% \pm 11.55\%$ ($\bar{x} \pm st.dev.$) higher than those from the cross section transects.

A paired t-test comparing mean scanning time for the cross section transect (19.00 ± 5.02 min, $\bar{x} \pm st.dev.$) to the longitudinal transect (7.41 ± 0.92) minutes was significant ($p < 0.001$). For an entire survey, the cross sections took an estimated 5 hrs 23 mins, compared to the longitudinal 2 hrs 1 min. That represents a time savings of 60.99% when actively surveying with the hydroacoustic gear. The travel time between transects remained constant, but the shorter scanning periods allowed for a noticeably shorter survey night.

Throughout the survey period, Rainbow Smelt and Cisco relative abundance remained stable (Figure 2.6). ANOVAs testing for differences of mean abundance by month and year were not significant for either Rainbow Smelt ($p = 0.61$) or Cisco ($p = 0.96$). August Rainbow Smelt estimates were slightly higher than July or September, but the difference was not statistically significant (Figure 2.7). Cisco estimates followed a similar pattern, but again this was not significant. Annually, there were no appreciable differences in abundance estimates for either species between the three months.

Discussion

We concluded the two transect methods generated similar interpolated abundance estimates. There was a tendency for the longitudinal transect density estimates to be higher than those from the cross sections, yet estimate precision was similar. This pattern might be expected, as the longitudinal transects targeted the pelagic zone and excluded littoral habitats where the two pelagic cold-water species were not present. The longitudinal transects were therefore considered preferable, as they generated similar relative abundance estimates post-data expansion while targeting cold water habitat with less time input. Differences in mean abundance between months were not statistically significant.

Hydroacoustic outputs used in this study were similar to those of Burczynski et al. (1987) and Fincel et al. (2016). We observed the same bimodal TS distribution, reflective of the bimodal length-frequency distribution. Our species assignment made similar assumptions, using the TS-length relationship. The assumption was simplified in

Lake Oahe because few species occupy the cold water hypolimnion. Additionally, few individuals overlapped with the adult Rainbow Smelt length-frequency distribution.

Gillnets are not widely used in the literature as an accompaniment to hydroacoustics for the purposes of fish community length-frequency determination, although several projects (Burczynski et al. 1987, Muska et al. 2011, Fincel et al. 2016) have demonstrated this approach. In our suspended gill nets, Cisco catches were higher than Rainbow Smelt (Figure 2.2), yet hydroacoustic total abundance estimates were generally similar (Figure 2.6). We suspect this may be due to greater gear efficiency of our nets for the larger Cisco. Deep water suspended gillnet efficiency for Rainbow Smelt has been a subject of debate within SDGFP (Lott et al. 2001). This would be problematic if we used gillnet catches as a relative abundance metric. As our goal was length-frequency determination, however, this is less of an issue.

We used a systematic survey design because of the evenness of survey coverage, an attribute which has contributed to the popularity of this design (Simmonds and MacLennan 2005). The design avoids the estimation challenges associated with continuous survey scanning, notably the partitioning of a single scan into smaller analysis units referred to as elementary sampling units (ESUs, Rudstam and Sullivan 2018). Sampling at systematic intervals did exclude reservoir areas between transects. The approach is unbiased if the underlying fish distribution is not periodic with transect spacing, a concept introduced by Cochran (1977). It is unlikely that the population exhibited an autocorrelative periodic structure with an 11.3 km frequency, concurrent with transect layout. This assumption is so specialized, it is generally not considered

(Petitgas 2001). The 11.3 km systematic transect spacing *a-priori* established the spatial scale of inference for interpolation. We used IDW interpolation, as this method performs well when sampling points are regularly spaced (Li et al. 2018). Additionally, a well understood advantage of IDW is sample measurements at a site are preserved, as opposed to model-based approaches (Chen et al. 2017). We used a distance threshold, constraining the interpolation of between-transect areas to the values of the bounding transects. Thus, an area's interpolated values became a gradient from one observation point to the next.

IDW does not perform well with clustered sampling points and is sensitive to the presence of outliers, which can generate an interpolated surface with isolated, concentric “bullseye” features (Li et al. 2018). If the bullseye phenomena occurred, it was considered to reflect a peak or trough in local fish density. Combined with the latitudinal elongate and relatively narrow reservoir morphology, bullseyes were laterally constrained by the reservoir shoreline. We therefore considered this phenomena to be minimally important, although results may vary in other systems. We assumed the method resulted in a reasonable approximation of fish population spatial structure.

Interpolation or prediction of fish distributions has been aided by the proliferation of GIS, remote sensing techniques, and many spatial analysis and modelling tools (Kery 2011). Hydroacoustic surveys, as a remote sensing technique, are well suited to these methods (Muska 2013), and options including neural network models (Brosse et al. 1999), geostatistical approaches (Taylor et al. 2005), and cluster analyses (Rinke et al. 2009) have been explored. Although IDW has been used in hydraulic modelling (Li et

al. 2018, Chen et al. 2017) and reservoir sediment accumulation (Simpson and Wu 2014), the authors are unaware of its use in fish relative abundance estimation from hydroacoustics. The method has no statistical assumptions, as the IDW equation is deterministic and user-defined. The major practical assumption, however, is the interpolation reflects the “real” fish distribution.

An alternative to the IDW interpolation method is kriging, thoroughly demonstrated by Taylor et al (2005). Kriging is especially useful when sample points are clustered (Petitgas 2001), a situation commonly arising from fish density clusters when the continuous scanning - ESU approach is used (Simmonds and MacLennan 2005). This creates a dense spatial network of sampling points with attendant clusters of high and low densities, and sometimes differing scales of variance structuring (Taylor et al. 2005). Kriging interpolates a surface based on the covariance structure of these points using weighted predictions from a fitted variogram model. In our case, the scale of inquiry was pre-established at 11.3 km by our transect spacing. Our sampling density was also relatively low given the large study survey area (68,500 ha) compared to other systems (e.g. 2,100 ha; Taylor et al. 2005). Kriging would require us to make assumptions about the nugget (or variogram γ -intercept), which is generally accepted as representative of spatial variation smaller than the scale of measurement and/or measurement error (Singh and Verma 2019). We would assume the nugget adequately described fish population structure within the 11.3 km distance lags between samples. As we have no means of evaluating that assumption, we consider it unreasonable. Kriging would also require fitting a complex, data-intensive model to a systematic, low density sampling

schema. Additionally, our goal was to provide an index of abundance, much like a CPUE, as opposed to a rigorous investigation of species spatial distribution. While IDW is simple compared to geostatistical and other computationally intensive techniques, that simplicity includes fewer assumptions and allows for easy explanation to the angling public, whose interest is a major factor in the Lake Oahe survey.

While estimates between survey months were not statistically different, it does appear that estimates for the later months were generally a bit higher. This may be due to strong vertical segregation of age-0 Rainbow Smelt from older conspecifics, as documented by Parker Stetter et al. (2006). They observed strong initial summer vertical segregation which declined in later months. As Rainbow Smelt cannibalism has been documented (Henderson and Nepszy 1989), thermal partitioning may aide in age-0 survival. Although biotic effects are generally secondary to abiotic influences on year class strength (Juza et al. 2014), predation avoidance by age-0 fish is nevertheless common. As age-0 Rainbow Smelt growth rates are generally high, potentially inflated by the loss of those fish that are not fast growing (Ganger 1999), cannibalism pressure may ease later in the summer. Combined with increasing body size and attendant shift in bioenergetic thermal niche from age-0 toward adult, thermal segregation may degrade later in the growing season leading to higher estimates as age-0 fish enter the adult depth range. Additionally, hydroacoustic studies of Lake Oahe Rainbow Smelt (Burczynski et al. 1987, Fincel et al. 2016), including this study, have not analyzed those regions above the mesotherm inhabited by age-0 Rainbow Smelt (Parker Stetter 2006). This may explain the seemingly higher estimates later in the season.

The method we demonstrated has limitations. As Rainbow Smelt populations generally are spatially clustered, our sampling interval may miss localized high or low clusters. This may lead to an overall abundance estimate that is skewed either high or low, depending on the clusters sampled. We consider slight inflations or deflations in the cold water abundance estimates as similar to site-specific variance influences on CPUE estimates. We do not consider this a rigorous investigation of Rainbow Smelt spatial distribution, and it should not be considered as such. We consider our method to be an efficient means of estimating general reservoir cold water prey abundance trends.

Management Implications

As Lake Oahe sportfish relative weights are highly responsive to Rainbow Smelt abundance (Graeb et al. 2008, Fincel et al. 2016b), our cold-water prey relative abundance estimates are part of a broader informational landscape. As summer Walleye condition is the integrator of the prey abundance throughout the reservoir, the cold-water prey estimates are generally considered imperative information. Here, we demonstrate a more efficient survey technique that was able to deliver estimates similar to a time-intensive alternative. A time savings of 60.99% provides a substantial savings to departments similar to SDGFP whose budgets have been tightening over time. More importantly, the time savings in running the survey equate to less time biologists are performing potentially dangerous work at night. Moreover, the ability for managers to move the survey to later summer months prevents “dry-dock” nights, or periods when biologists are unable to sample due to severe weather events more commonly experienced in July and early August.

As estimation and analytical techniques become ever-more complex within the fisheries literature, we hope that our intentionally simplified approach demonstrates the continuing utility of clear, easy-to-comprehend methodologies and metrics to the fisheries management process.

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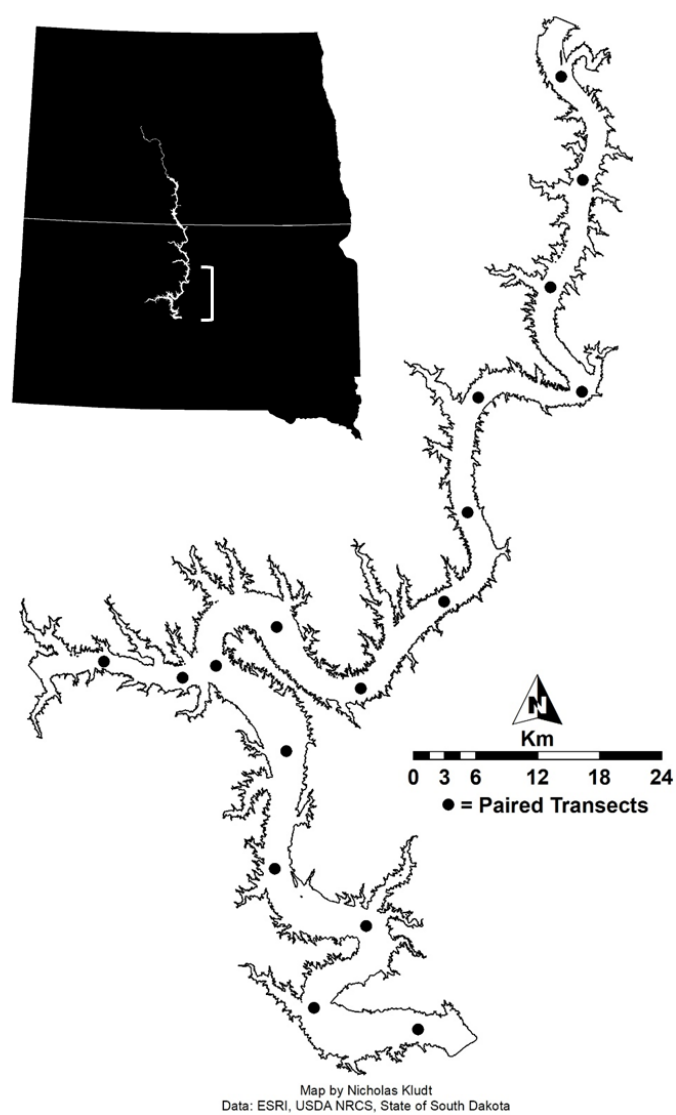


Figure 2.1: Stratified lower zone of Lake Oahe, South Dakota. Inset shows position within North and South Dakota, with the study area in South Dakota bracketed.

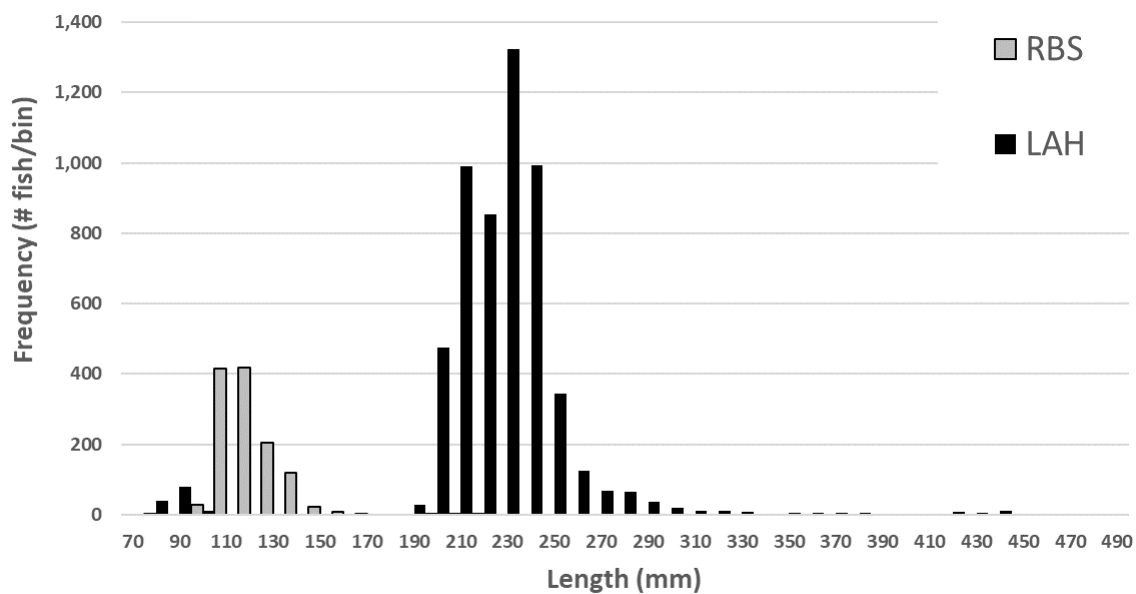


Figure 2.2. Length-frequency distribution of Rainbow Smelt (RBS) and Cisco (LAH) collected during targeted cold water suspended gillnetting, Lake Oahe, South Dakota 2012-2018.

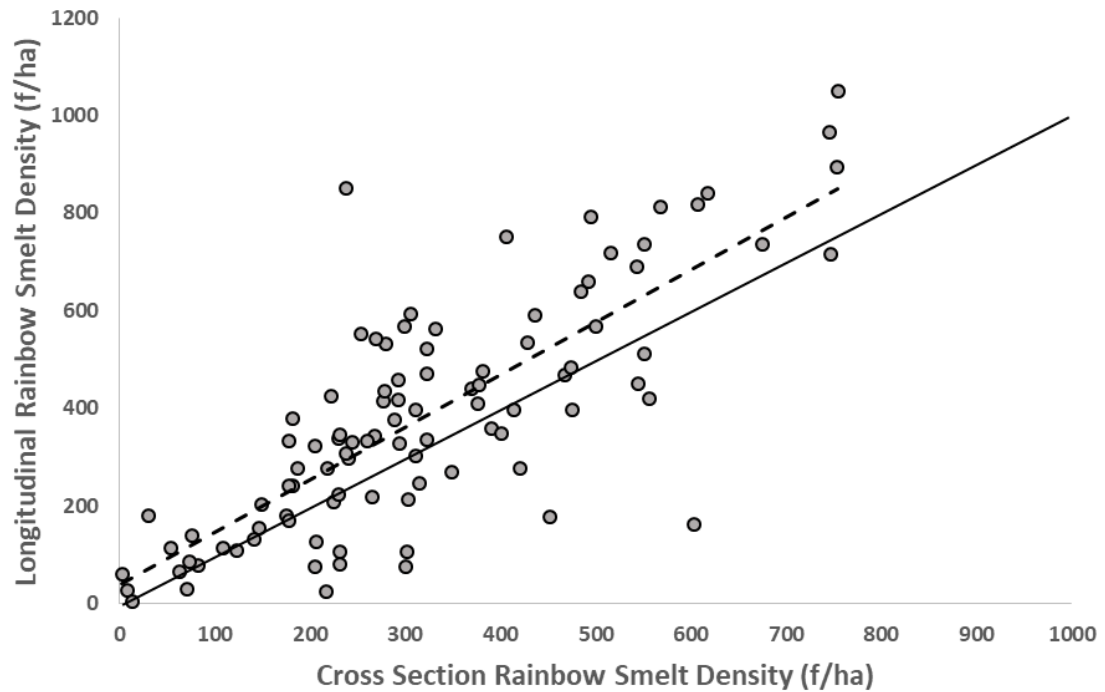


Figure 2.3. Linear regression comparing Rainbow Smelt density estimates from two hydroacoustic transect designs, Lake Oahe, South Dakota 2015-2018. The dashed line is the regression ($p < 0.001$, $F = 158.59$, $df = 96$, $\text{adj.}r^2 = 0.62$), while the solid black is a 1:1 line. Longitudinal transects were oriented over and parallel to the historic channel, and cross section transects were perpendicular to the shoreline, bisecting the reservoir.

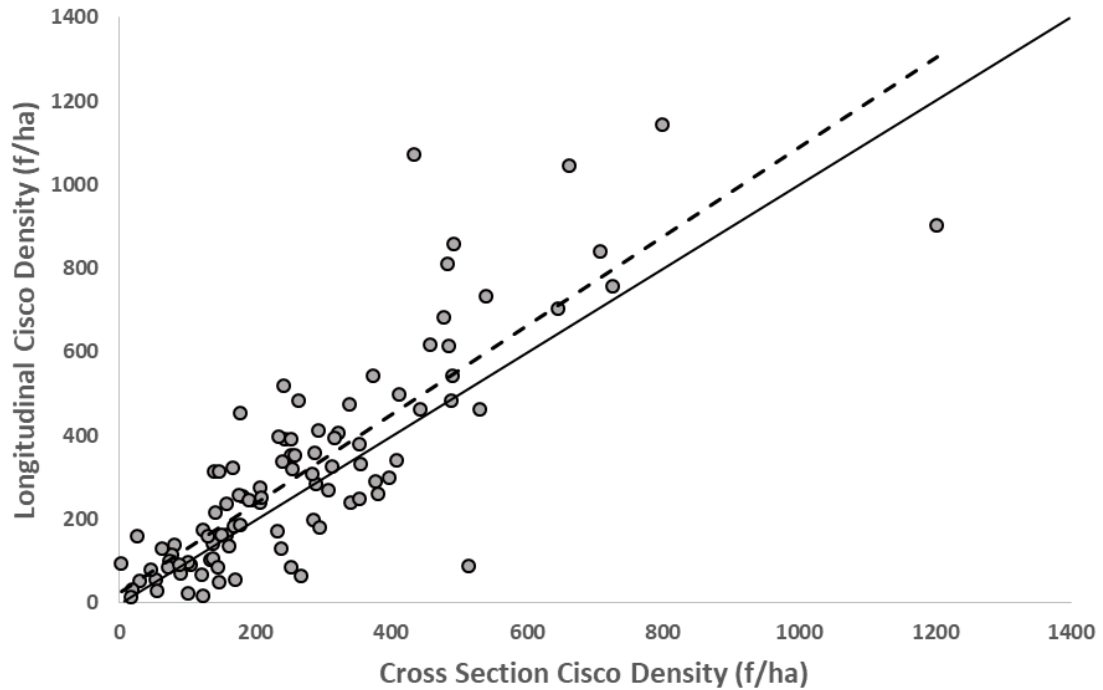


Figure 2.4. Linear regression comparing Cisco density estimates from two hydroacoustic transect designs, Lake Oahe, South Dakota 2015-2018. The dashed line is the regression ($p < 0.001$, $F = 209.48$, $df = 96$, $\text{adj.}r^2 = 0.68$), while the solid black is a 1:1 line.

Longitudinal transects were oriented over and parallel to the historic channel, and cross section transects were perpendicular to the shoreline, bisecting the reservoir.

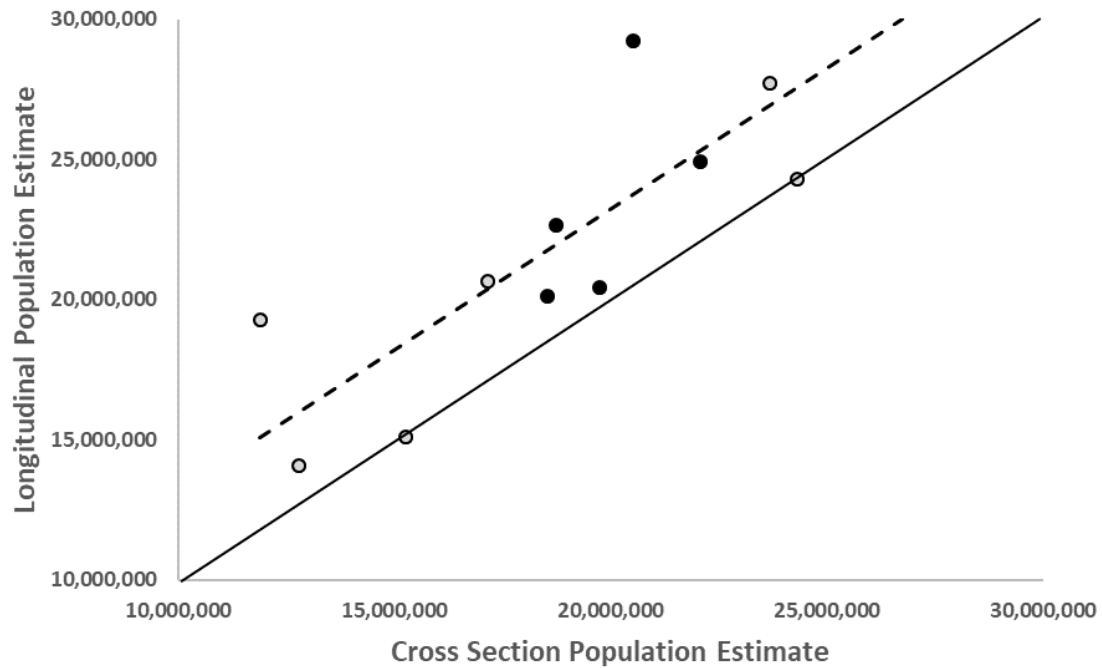


Figure 2.5. Linear regression comparing population abundance estimates from two hydroacoustic transect designs, Lake Oahe, South Dakota 2015-2018. Solid black circles are Rainbow Smelt estimates, grey circles are Cisco. The dashed line is the regression ($p < 0.001$, $F = 26.57$, $df = 96$, $\text{adj.}r^2 = 0.70$), while the solid black is a 1:1 line. Longitudinal transects were oriented over and parallel to the historic channel, and cross section transects were perpendicular to the shoreline, bisecting the reservoir.



Figure 2.6: Rainbow Smelt (black) and Cisco (grey) abundance trends, Lake Oahe, South Dakota, summers 2015-2018. Survey periods are labelled month-year (J-July, A-August, S-September).

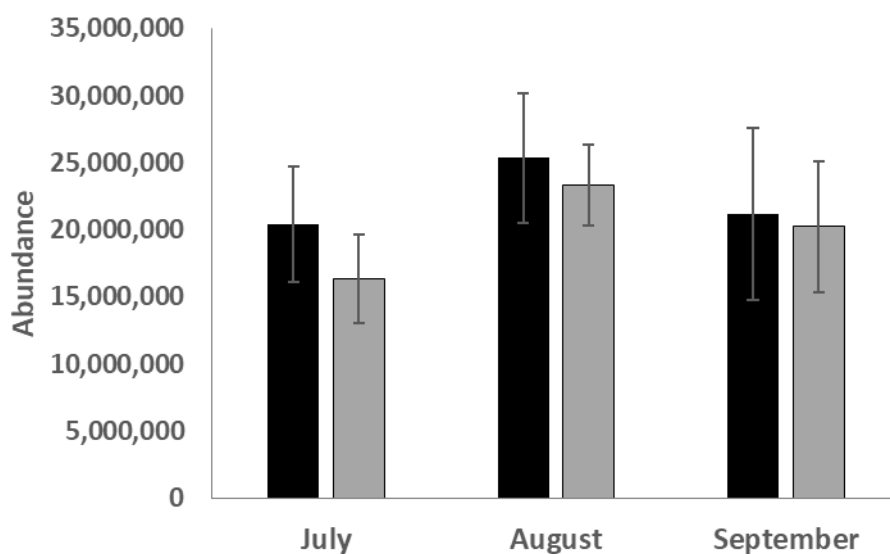


Figure 2.7: Mean annual abundance estimates (\pm 95% confidence interval) by month for Lake Oahe Rainbow Smelt (black) and Cisco (grey), 2015 – 2018.

Table 2.1: Mean square error (MSE) variance components and linear regression estimates \pm 95% Bonferroni adjusted confidence intervals, comparing paired density observations from longitudinal and cross section transect designs. For MSE variance decomposition, the mean components are differences between paired values, slope component is deviation from unity (1:1 fit), and residual component is random error.

	Rainbow Smelt	Cisco
Mean (Z)	0.02	0.08
Slope (S)	0.30	0.37
Residual (R)	0.67	0.55
Slope	0.58 ± 0.11	0.65 ± 0.10
Intercept	98.05 ± 47.32	68.84 ± 40.80

Table 2.2. Mean square error (MSE) variance components and linear regression estimates \pm 95% Bonferroni adjusted confidence intervals, comparing interpolated abundance estimates from longitudinal and cross section transect designs. For MSE variance decomposition, the mean components are differences between paired values, slope component is deviation from unity (1:1 fit), and residual component is random error.

Mean	0.61
Slope	0.10
Residual	0.30
Slope	0.72 ± 0.37
Intercept	$3,023,078 \pm 8,523,019$

CHAPTER 3: DETERMINING LAKE OAHE, SOUTH DAKOTA, COLD-WATER FISH POPULATION DISTRIBUTION AND HYDROACOUSTIC SURVEY COVERAGE

Abstract

Hydroacoustic sampling is commonly used to estimate the abundance or biomass of pelagic species. Large magnitudes of variability are a hallmark of hydroacoustic data and occur due to scanning of heterogeneously distributed fish populations. Spatial structuring of fish population distribution affects relative abundance estimates, but also reflects underlying processes driving distribution. These dynamics complicate the process of determining adequate sample size for abundance estimation. We therefore sought to understand the spatial patterning of the pelagic cold-water forage fish Rainbow Smelt *Osmerus mordax* in Lake Oahe, SD, a large Missouri River reservoir. We analyzed the results of a systematic hydroacoustic survey using Moran's i and Getis-Ord General G statistics, followed by local integrated spatial autocorrelation (LISA) mapping and Getis-Ord G hotspot analysis to visualize patterns. These revealed significant spatial structuring of Rainbow Smelt populations, with annual spatial clusters emerging. We then incorporated spatial population structure into an assessment of survey sample size adequacy, assessed by bootstrapped estimates of zonal mean Rainbow Smelt density. Bootstrapped means did not differ over a range of potential survey effort, thus indicating that present sampling coverage is adequate.

Introduction

Fisheries managers often use relative abundance metrics to manage fish populations, commonly expressed as catch per unit effort (CPUE), yet CPUE data are notorious for high variability (Hubert and Fabrizio 2007). Environmental conditions, seasonality, and fish behavior are among the many potential sources of variance. Population distribution as a result of spatial processes can also inflate variability (Hulbert 1984). These underlying processes, also known as spatial autocorrelation, can lead to inappropriate sampling designs if left unaddressed (Lengendre et al 2004).

Mobile hydroacoustic surveying is an active sampling technique that is susceptible to spatial autocorrelation. Hydroacoustic surveys generate estimates of fish density for a given sonar scan. As mobile hydroacoustic surveys typically cover large areas, they encompass heterogeneously distributed fish populations. The clusters of high and low density, while representative of the spatial distribution of fish, lead to large magnitudes of variability (Simmonds and MacLennan 2005). To improve estimates, the classic design-based approach is an evaluation of sample size. Using statistics that describe population distribution, a system can be stratified according to spatial patterning. Stratification can minimize the variance inflation from factors underlying the observed distribution (Quinn and Keough 2002). In reservoir systems, fish distribution is often variable along productivity gradients or zones (Wetzel 2002, Fincel 2011). Consequently, sample size estimation within reservoir spatial strata should yield more reliable estimates for managers.

Hydroacoustic sampling is commonly used to estimate the abundance or biomass of pelagic species (Parker-Stetter et al. 2006, Simmonds and MacLennan 2005). The amount of effort necessary for high-quality estimates varies by system and survey objectives. Although some research offers *a-priori* guidance on acceptable levels of hydroacoustic sampling effort (Aglen 1983, Aglen 1989), there remains no standard guidance on the topic (Simmonds and MacLennan 2005). Thus, hydroacoustic practitioners must, on a case-by-case basis, consider the classic dilemma of fisheries monitoring; balancing survey time, cost, and estimate quality.

Rainbow Smelt *Osmerus mordax* are a pelagic, cold water forage fish that have been widely sampled using hydroacoustics. The hydroacoustic properties of the species have been well documented (Parker Stetter et al 2006, Burczynski et al. 1987, Fincel et al. 2016). In Lake Oahe, South Dakota, Rainbow Smelt are the primary forage for a regionally important Walleye *Sander vitreus* sport fishery, with Walleye condition highly dependent on Rainbow Smelt abundance (Graeb et al. 2008). The Rainbow Smelt population, which is surveyed annually in July with a mobile hydroacoustic survey, has anecdotally displayed consistent distributional patterns over the 18-year history of the survey (South Dakota Department of Game, Fish, and Parks (SDGFP), unpublished data). As part of a larger effort to optimize the hydroacoustic survey protocol, we sought to 1) define Rainbow Smelt population spatial structure to determine biologically relevant reservoir strata, so 2) we could estimate the appropriate level of within-strata sampling effort for the survey.

Methods

Study area – Lake Oahe is the second largest storage reservoir on the Missouri River, stretching 372 km from central North Dakota to central South Dakota (Figure 3.1). At normal pool, Lake Oahe's surface area measures 145,000 ha. The upper portion of Lake Oahe in South Dakota is mesotrophic, and transitions to oligotrophic downstream toward the dam (Fincel 2011). The reservoir stratifies during the summer months, with the northern extent of stratification typically occurring just upstream of the Moreau River tributary arm (River Mile 1177, Burczynski et al. 1987, SDGFP, unpublished data). The Cheyenne River tributary arm shallows in its western extent, and the stratified zone within this region varies by year and month. Cold water species are thereby constrained to the lower 169 km of Lake Oahe, an approximate area of 68,500 ha (Figure 3.1).

Hydroacoustic surveys – We designed a systematic layout of cross-sectional transects ($n = 34$), spaced every 5.6 km and covering the stratified reservoir zone (Figure 3.1). The survey was repeated annually in July, 2015-2017. In 2015, 2 transects were not completed due to inclement weather. Multiple nights were required to complete each survey, with each night's work commencing a minimum of 30 minutes after sundown. This removed consideration of diel vertical Rainbow Smelt migrations (Fincel et al. 2016, Appenzeller and Leggett 1992) and eased fish target discrimination later in analysis (Burczynski et al. 1987). We surveyed between the waning lunar third quarter and the waxing lunar first quarter to avoid potential ambient light level effects on fish behavior (Appenzeller and Leggett 1995). For the same reason, all surveys were run with vessel lights off, with the exception of required navigational lights.

Hydroacoustic surveys were conducted using a Biosonics DT-X system with a 420 kHz split beam transducer set up for vertical beaming. The transducer had a 6.9° circular beam angle and was mounted to the side of the survey vessel on an adjustable arm. Survey settings were 5 pings/s with a pulse duration of 0.5 ms. System calibration was periodically checked according to the manufacturer's instructions using a 17.5 mm tungsten carbide target sphere and the apparatus described by Foote et al. (1987). Data were analyzed using the single echo detection biomass option with 40-log(R) time varied gain within Sonar5-Pro (Balk et al. 2015), due to low overall pelagic target densities. We excluded a 0.5 m layer immediately above the lakebed to eliminate bottom interference (Parker Stetter et al. 2006, Simmonds and MacLennan 2005). We used the TS equation from Love (1977) to convert TS to approximate fish length and subsequently assign a species identification:

$$TS = 19.4 * \log_{10}(TL) - 0.9 * \log_{10}(f) - 62$$

where *TS* is the target strength of an individual fish, *TL* is the total length (cm) of the fish, and *f* is the frequency of the sonar pulse in kilohertz. We assigned individuals' TS-length to species based on length frequencies from annual deep-water gill netting conducted 2012-2018, following Fincel et al. (2016). Rainbow Smelt were vertically constrained by temperature during July due to reservoir stratification, and species assignment of acoustic targets was limited to targets below or within the mesothermal layer. In Lake Oahe, few species occupy the cold water hypolimnion, and there is minimal overlap of size distribution between the pelagic cold-water species. We used the percent of fish that were age-1+ Rainbow Smelt in each 10-mm length grouping

from gill net length-frequency distribution to designate targets as age 1+ Rainbow Smelt based on the estimated target size from the TS-length regression. Within Sonar5-Pro, the sampled beam area (ha) was determined, fish density was quantified (fish/ha), and a density was assigned to the transect centroid for further analyses.

Spatial Pattern Analyses - Our goal was to produce annual estimates of Rainbow Smelt abundance, and maps of distribution. Given the spatial data requirement, we accepted a minimum sampling paradigm based on species distribution. Distribution mapping requires samples to be located at intervals less than the range of spatial autocorrelation (Simmonds and MacLennan 2005). We therefore needed to determine the distance of that range for survey design purposes. Additionally, we needed to examine spatial clustering within the reservoir for sample size estimation. Based on clustering, the reservoir could be divided into zones. Within the zones, we could estimate sample sizes required to generate an accurate estimate of the zonal mean density.

We used Moran's i to evaluate the range of autocorrelation and local integrated spatial autocorrelation (LISA) to map population clusters. Moran's i tests the null hypothesis that spatial autocorrelation of a variable is zero (Ord and Getis 1995). This involves correlations between pairs of observations by distance, and complications immediately arose from Lake Oahe's complex shape. To remove the influence of inconsistent Euclidean distances between points, especially noticeable around major reservoir bends and peninsulas, we converted the spatial layout of transects to a subway map (Monmonier 1996). We used Army Corps of Engineers river mile values for our Y coordinates, with a zero X coordinate on the main reservoir. The Cheyenne river

arm Y values remained consistent with the confluence river mile, with X coordinates as river miles west of the confluence with the reservoir (Figure 3.1). The simplified spatial layout of transect centroids and connectivity matrix solved the Euclidean distance problem. For Morna's i and LISA analyses, we used SAM: Spatial Analysis in Macroecology (Rangel et al. 2010). We used a Moran's $i \geq 0.2$ threshold ($\alpha = 0.05$) to evaluate if significant local autocorrelation existed within a given distance class (Gangl and Whaley 2005, Kludt et al. 2017). Hotspot maps of Moran's i LISA values were also generated using SAM to help determine reservoir zonation.

To further evaluate spatial clustering of observations after the global and local Moran's i analysis, we used the Getis-Ord General G statistic, followed with Getis-Ord G hotspot mapping in ArcGIS 10.4 (ESRI 2016). The G statistic is generally thought to be more sensitive to distance clusters than global Moran's i (Ord and Getis 1995), and although distance can be temporal, genetic, etc., we use it geographically. The subway map layout was used for analysis, with 2 fixed Euclidean distance bands, based on the coordinate system previously described. Distance band selection was based on the LISA and Moran's i results. Using LISA and Getis-Ord hotspots, we divided the reservoir into 2 zones between transects 12 and 13 (Figure 3.3). The transect blocks in the lower reservoir ($n = 15$) and upper reservoir ($n = 19$) zones were then used for subsequent sample size estimation.

We used two sample size estimation methods, and compared the results. The first was a Student's t -distribution sample size estimator based on descriptive statistics

(Zar 1999). In this exercise, we conceptualized the hydroacoustic densities as a catch per unit effort statistic. The estimator is given by the equation:

$$n_r = \frac{(t)^2 * (s^2)}{(a * \bar{x})^2}$$

where n_r is the sample size required, t is a t -value for $(n_{samples} - 1)$ degrees of freedom, s^2 is the variance, a is the acceptable error in describing the mean, and \bar{x} is the zonal mean CPUE. We used $\alpha = 0.2$, as the 80% confidence level is frequently used for CPUE trend analysis by SDGFP managers thus making it appropriate for our estimation of mean density.

Second, we bootstrapped a zonal mean for a range of sample sizes. Using a parametric bootstrap method in the “resample” R package (Hesterberg 2015, R Core Team 2018), we sampled with replacement ($n_{iterations} = 10,000$) to generate a simulated zonal mean, with an associated bootstrap 95% confidence interval. The 95% confidence interval was calculated using the bootstrap percentile method (BPI), which generally performs well due to insensitivity to data skewness or kurtosis (Kenner-Cohen et al. 2017, Hall 1988). We used 8 as the minimum bootstrap sample size, as this is the minimum sample size on which a bootstrapping is generally recommended (Chernick 2007), thereby representing a reasonable cutoff for a minimum zonal sample size.

Results

Fish surveys – Gillnetting data showed Rainbow Smelt length-frequency distribution consistently did not overlap with other species below the mesothermal layer.

Additionally, results were consistent from 2012-2018, allowing us to pool the catch data.

While a degree of overlap existed in the 100 mm size bin between small adult Rainbow

Smelt (72%) and age-1 Cisco (28%), Rainbow Smelt were the only species within the 110 – 180 mm size bins during the 7 years of gillnetting (Figure 3.2). We therefore classified acoustic targets 100-180 mm as Rainbow Smelt age-1+, with a proportional correction for the 100 mm bin.

Rainbow Smelt densities in the reservoir showed some consistent spatial patterns (Figure 3.3). Densities were uniformly depressed in the lower reaches of Lake Oahe. Near the central portion of the study area, the Cheyenne River enters the reservoir and forms a major tributary arm. Immediately downstream of this area is an area of generally higher density that was stable across the 3 survey years. This region recorded the highest density in 2016. Upstream of the Cheyenne arm, Rainbow Smelt density was variable, with local areas of high density. Distribution of high-density areas shifted from year to year. The highest densities recorded in 2015 and 2017 occurred in this area.

The spatial clustering analyses used the subway map of transect centroids to focus on just the spatial population structure, as the geometry of the reservoir induced linkages across several “S”-bends (Figure 3.1). This was avoided with the subway map layout. The Moran’s i analysis, examining the spatial autocorrelation range, revealed significant clustering in 2015 ($i = 0.377$, $p = 0.005$) and 2017 ($i = 0.313$, $p = 0.010$). No significant spatial structuring was detected in 2016, as Moran’s I values for all distance classes remained below the 0.2 threshold (Figure 3.4), so 2016 was not carried forward for LISA analysis. The autocorrelation range for 2015 and 2017 was significant at less than 10 map distance units, equivalent to 16 km (Figure 3.4). Over the 0-10 distance unit

range, the strength of autocorrelation declined steadily, until it fell below the 0.2 threshold. The Rainbow Smelt transect density was influenced by immediately upstream and downstream transects (+1, -1), with a smaller amount of influence displayed by the next pair of transects, moving outward (+2, -2). The 2015 LISA heat map highlighted a mid-reservoir cluster (Figure 3.5), corresponding to an area of relatively higher density (Figure 3.3). The 2017 LISA heat map highlighted a cluster on the low end of the reservoir near the dam, which were the lowest densities recorded that year. There was no major structuring of highs or lows in the vicinity of the Cheyenne Reservoir arm.

Based on the Moran's i spatial autocorrelation range of 10 map units and (+2, -2) transect influence, we applied the Getis-Ord General G at 3.5 and 7 map unit distance bands. Both bands showed significant spatial clustering over all three years (Table 3.1). The 3.5 map unit hotspot map highlighted the elevated clusters of Rainbow Smelt density, with high fidelity of clusters (Figure 3.6) to visual assessment of the raw data (Figure 3.3). The same clusters are evident in the 7 map unit hotspots (Figure 3.7), with a relatively wider cluster extent. Again, there was no major cluster spanning the area upstream and downstream of the Cheyenne arm.

Given this pattern was observed with both spatial analyses, we divided the reservoir into two zones at transect 12 (Figures 3.3, 3.6, 3.7), with the "lower zone" defined as transects in the Cheyenne arm, at the confluence with the reservoir, and south to the dam ($n = 15$). The upper zone contained all transects north of the Cheyenne confluence ($n = 19$). For the bootstrap resampling, we wanted two zones with a roughly

equal number of transects and surface area. We also did not want the zonal division to disrupt any high or low density clusters, and felt this location accomplished this.

Within these zones, we first applied the t-distribution sample size estimation technique. It was predicted the upper zone required fewer transects than the lower zone, with approximately half the effort if the predictions were averaged (Table 3.2). The upper zone also showed less relative variance than the lower zone. The lower zone had increased variance due to the difference between the relatively stable, moderate densities immediately downstream from the Cheyenne arm, and the relatively stable, extremely low densities near the dam.

The bootstrapped resampling yielded similar results for the upper reservoir. Bootstrapped mean densities were created for sample sizes of 19 to 8 samples. The means were steady across all sample sizes, with similar variance within the bootstrapped sample. There was no appreciable advantage to sampling more than 8 transects in this zone, as the range of potential means within the 95% bootstrap confidence interval as consistent across sample sizes (Figure 3.8).

The lower reservoir bootstrap predictions were similar to those for the upper reservoir but were different from the t-distribution sample size estimation. Bootstrapped mean densities were created for sample sizes of 15 to 8 samples. The mean density was similar across all simulated sample sizes, with similar variance ranges again observed. While the t-estimator was heavily influenced by the zonal variance and the need for more samples to increase power, the bootstrapped estimation showed

that sampling in the region at the current effort level could be reduced to 8 transects with similar predicted variance.

Discussion

Determining the level of effort necessary for a survey is not unique to fisheries hydroacoustics. Hydroacoustic sampling, however, is unique because it directly measures fish density estimates as a function of acoustic targets to the volume of water ensonified during the sampling frame. Our species assignment to acoustic targets followed the methods of Burczynski et al. (1987) and Fincel et al. (2016). Target strengths were similar to those studies and the bimodal TS distribution was assumed to be reflective of a bimodal length-frequency distribution (Figure 3.2), with species assigned accordingly. As individual hydroacoustic transects yield fish densities, we conceptualized that density estimate as a CPUE, similar to trawling samples. Elementary sampling distance units (ESDUs) are the spatial scale of inquiry to which a hydroacoustic density relates (Simmonds and MacLennan 2005). In the case of individual hydroacoustic transects within a survey, we conceptualized the ESDU as the entire transect, with the estimated density/CPUE relating to the centroid of that transect. We further conceptualize the estimated density/CPUE as a value that can be averaged, much as site-specific CPUEs are averaged for a lake, with the variance estimators about the mean describing variance for a given area.

Our approach using autocorrelation and hotspot analyses to delineate Rainbow Smelt population distribution strata is unique in hydroacoustic research. The progression is similar, however, to other hydroacoustic survey design investigations

using spatial statistics (Taylor et al. 2005). Conversely, Aglen (1983, 1989) attempted to empirically quantify the extent of hydroacoustic survey coverage necessary to minimize the overall survey coefficient of variation. His idea was based on a ratio of area available to survey area. Despite successful use by Godlewska et al. (2009) in a set of Polish lakes, Aglen's method was never widely adopted, as population distributions often vary widely between systems and are more appropriately assessed on a case-by-case basis (Simmonds and MacLennan 2005).

Both stratification methods captured the lower abundances clustered in the lower reservoir near the dam. This is consistent with reservoir productivity zonation as demonstrated by Fincel (2011) in Lake Oahe using chlorophyll α , total phosphorus, Kieldalv nitrogen, and cladoceran density, with depressed values in the lower reservoir relative to upstream sites. As Rainbow Smelt in Lake Oahe are zooplanktivorous (Karnitz 1992), the depressed abundances in the lower reservoir cluster may broadly be the product of reservoir productivity gradients.

Entrainment may also contribute to the lower relative abundances on the lower reservoir. Occasional floods, with attendant high discharges, lead to massive Rainbow Smelt entrainment and bust cycles in the Lake Oahe population (Fincel et al. 2016). In years with routine discharge, high consumption of Rainbow Smelt by Walleye and Smallmouth Bass has been observed below Oahe Dam (Wuellner et al. 2010), hinting at some level of "normal" entrainment, as the Lake Oahe tailrace does not support a naturalized Rainbow Smelt population. While some level of entrainment occurs annually, it is unlikely that it is solely responsible for the depressed abundances in the

lower third of the reservoir. Instead, entrainment likely acts in conjunction with the large-scale reservoir productivity patterns previously discussed.

Our results suggested overall sampling effort could be reduced. The t -statistic sample size estimator suggested more sampling effort is necessary in the lower end of the reservoir, an area of low population density. Conversely, the bootstrap simulations showed this would have little effect on density estimates and variability. Low density populations generally require more sampling effort for a given level of accuracy, and this can be exacerbated in homogeneous environments (Angermeier and Smogor 1995). Rainbow Smelt pelagic movement likely reflects foraging behavior. We assume constant movement is the result of constantly changing resource distribution; thus, it is unlikely that Lake Oahe Rainbow Smelt inhabit a homogeneous environment, even in areas of low density. Peterson and Rabeni (1995) showed fewer samples are required to precisely estimate community-level attributes than individual species population attributes when all stream habitats in a reach were sampled. Our results may be similar due to our conceptualization of a site CPUE as inclusive of all habitat types within the transect scan path (e.g. nearshore, pelagic, etc.). Conversely, we showed estimation of a species-level attribute was not improved with greater effort, perhaps indicating broad-scale acoustic sampling is more similar to broad community-level descriptors. This is similar to gear and effort comparisons that highlight differential levels of effort and precision from different gears (Jackson and Harvey 1997) and different spatial scales (Kennard et al. 2006). Simulations of electrofishing transect effort have shown it is reasonable to use a single level of effort for CPUE estimation unless density becomes

very low (Kershner and Marschall 1998), which may indicate the areas of low density found in this study have not fallen below some critical point whereby increased sampling density might yield improved results.

Management Implications

We presented an approach to sampling stratification that has not been previously applied to hydroacoustic survey design. This is partially because our design is not a continuous survey and is instead a series of discrete transects. Accordingly, our analyses of acceptable survey coverage were *ex post facto* and more closely resemble stratification of more traditional gears.

Ultimately, spatial structuring of fisheries is common (Berger 2017), and understanding these complexities informs better monitoring and management decisions. Our investigation highlighted the spatial structure of Rainbow Smelt in Lake Oahe, and revealed the ability to substantially reduce survey effort. We recommend the adoption of a sampling scheme with 8 transects per zone, as we have shown similar estimates density and attendance variance across sampling intensity. A reduction in transects ($n = 16$) represents a substantial cost and effort savings compared to the intensive transect layout ($n = 34$). Rainbow Smelt in both zones of the reservoir could be adequately described using hydroacoustics in approximately half the effort of the intensive design used for this study.

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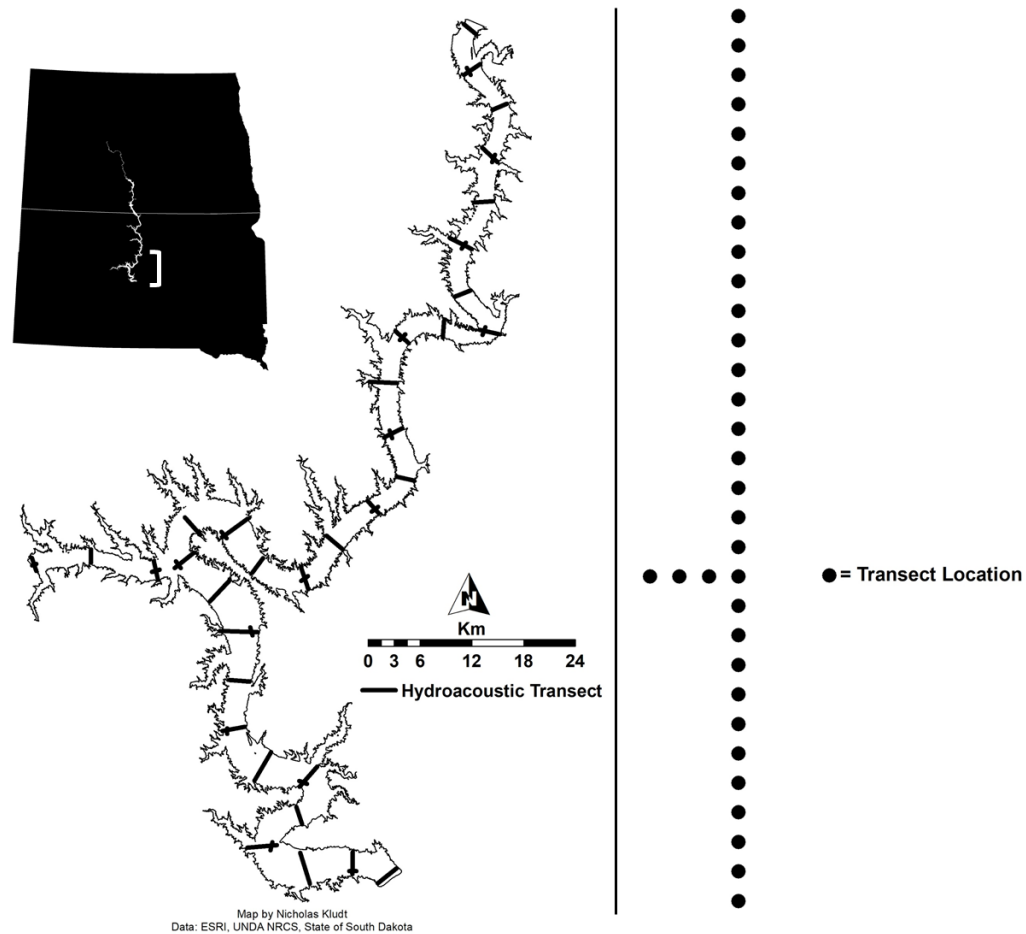


Figure 3.1: Hydroacoustic transect locations in the stratified lower zone of Lake Oahe, South Dakota (left). Inset highlights study area relative to North and South Dakota. Subway map simplification of study area geometry (right), shown for comparison.

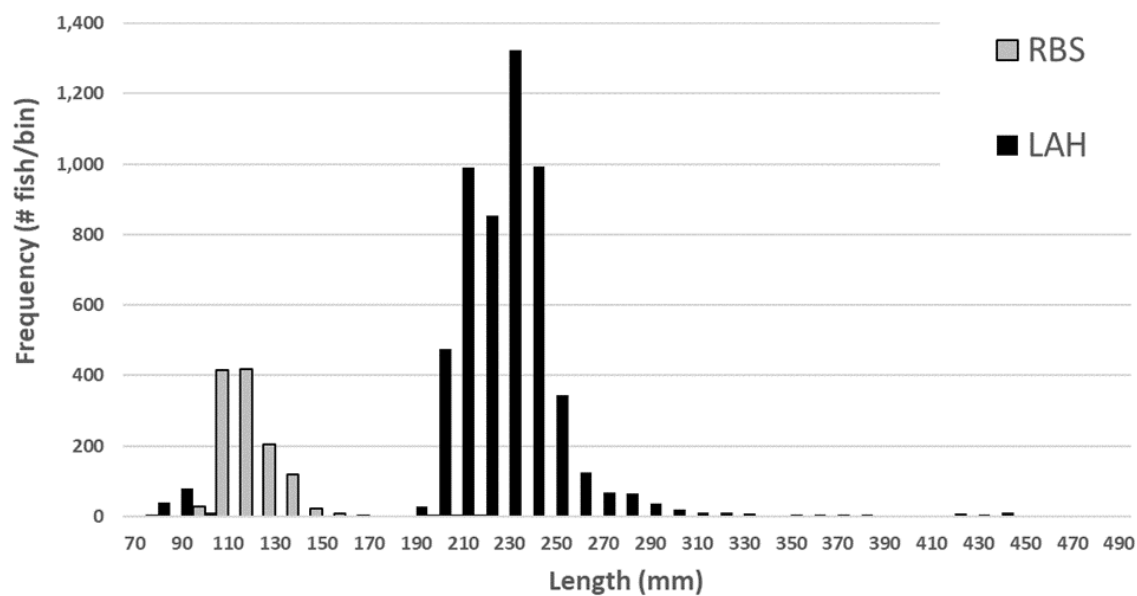


Figure 3.2: Length-frequency distribution of Rainbow Smelt (RBS) and Cisco (LAH) collected during targeted cold water suspended gillnetting, Lake Oahe, 2012-2018.

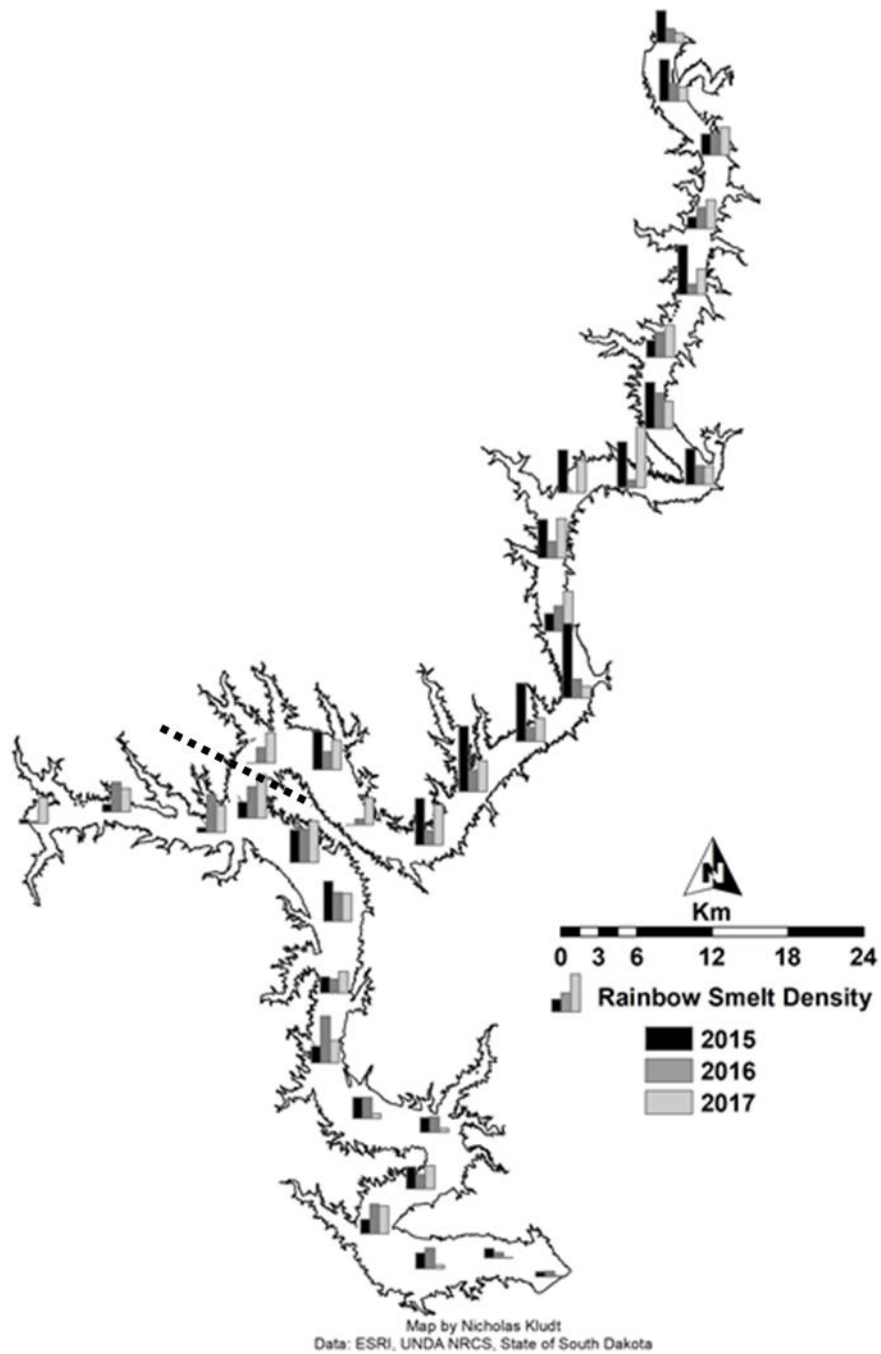


Figure 3.3: Rainbow Smelt density (f/ha) from July hydroacoustic surveys, 2015-2017, Lake Oahe, South Dakota. The dashed line represents our reservoir zone division.

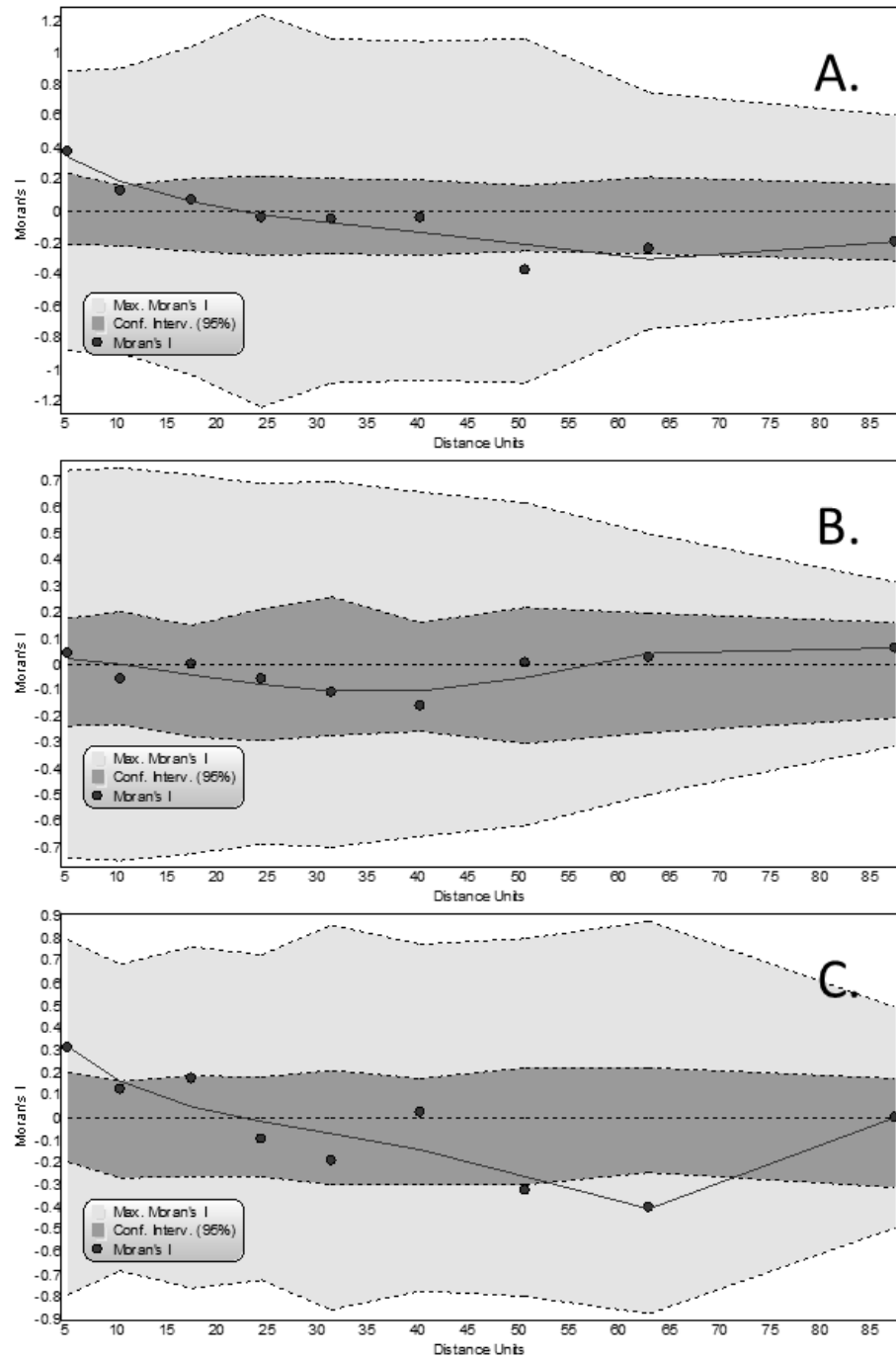


Figure 3.4: Moran's i correlograms of Rainbow Smelt transect densities across distance classes, (A.) 2015, (B.) 2016, (C.) 2017.

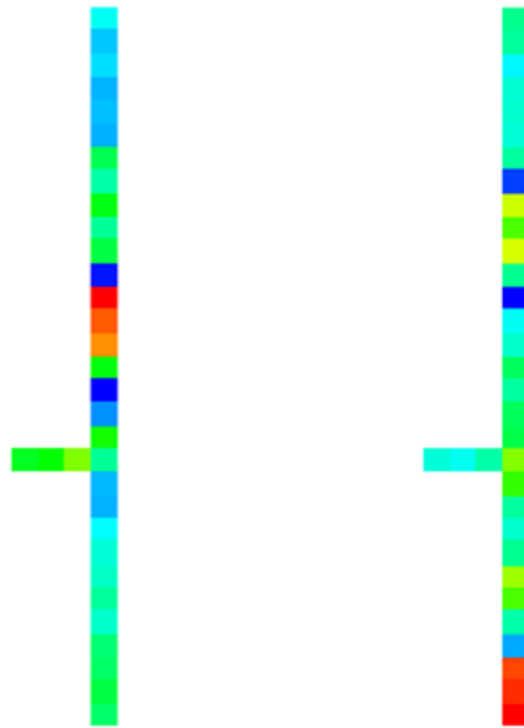


Figure 3.5: LISA heatmaps of Rainbow Smelt density clustering, 2015 (left) and 2017 (right), Lake Oahe, South Dakota. Each pixel represents an individual transect. Cooler colors represent low local Moran's i values, while warmer colors represent higher values.

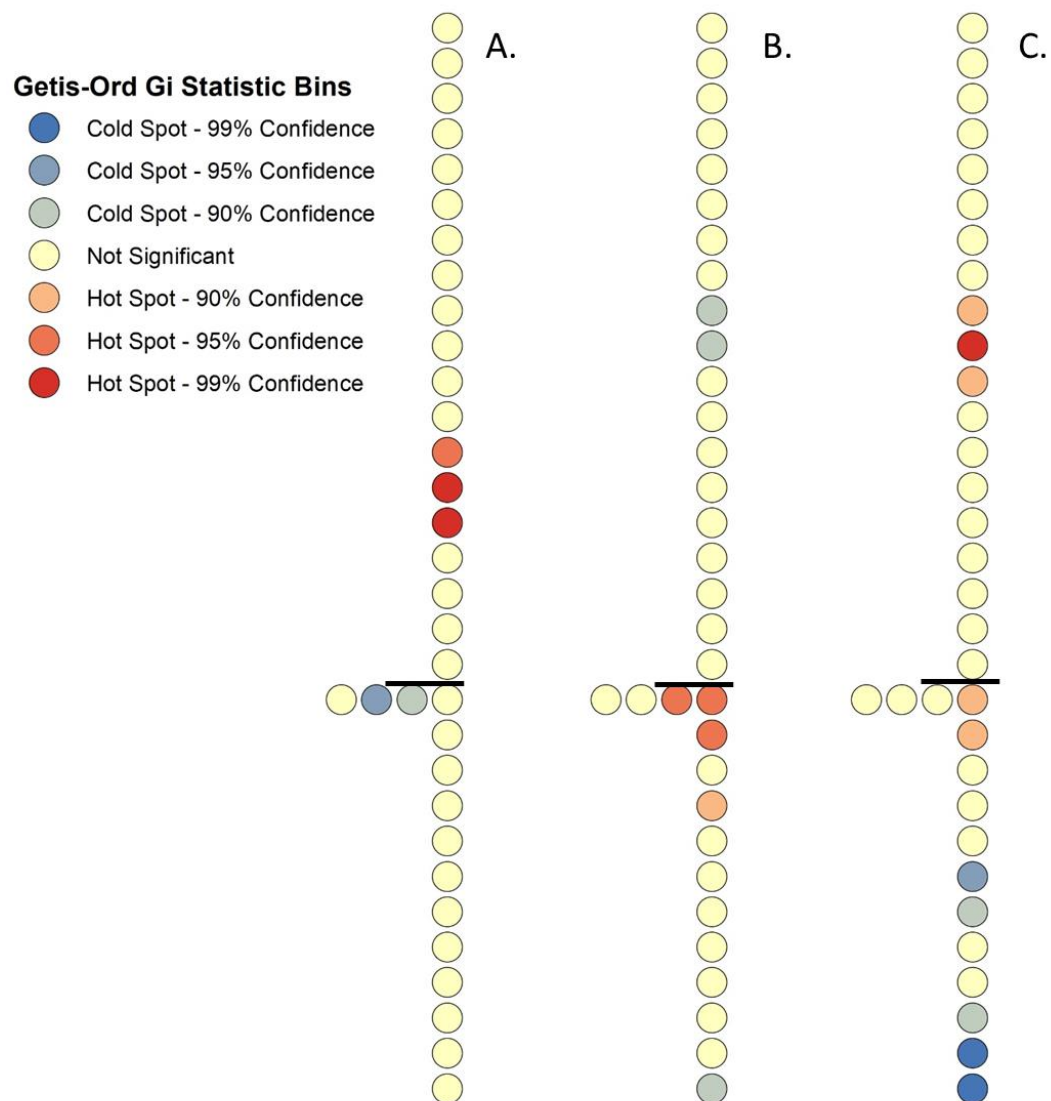


Figure 3.6: Getis-Ord General G spatial clustering of Rainbow Smelt density at 3.5 map units, (A.) 2015, (B.) 2016, (C.) 2017. The black bars denote the reservoir zone division.

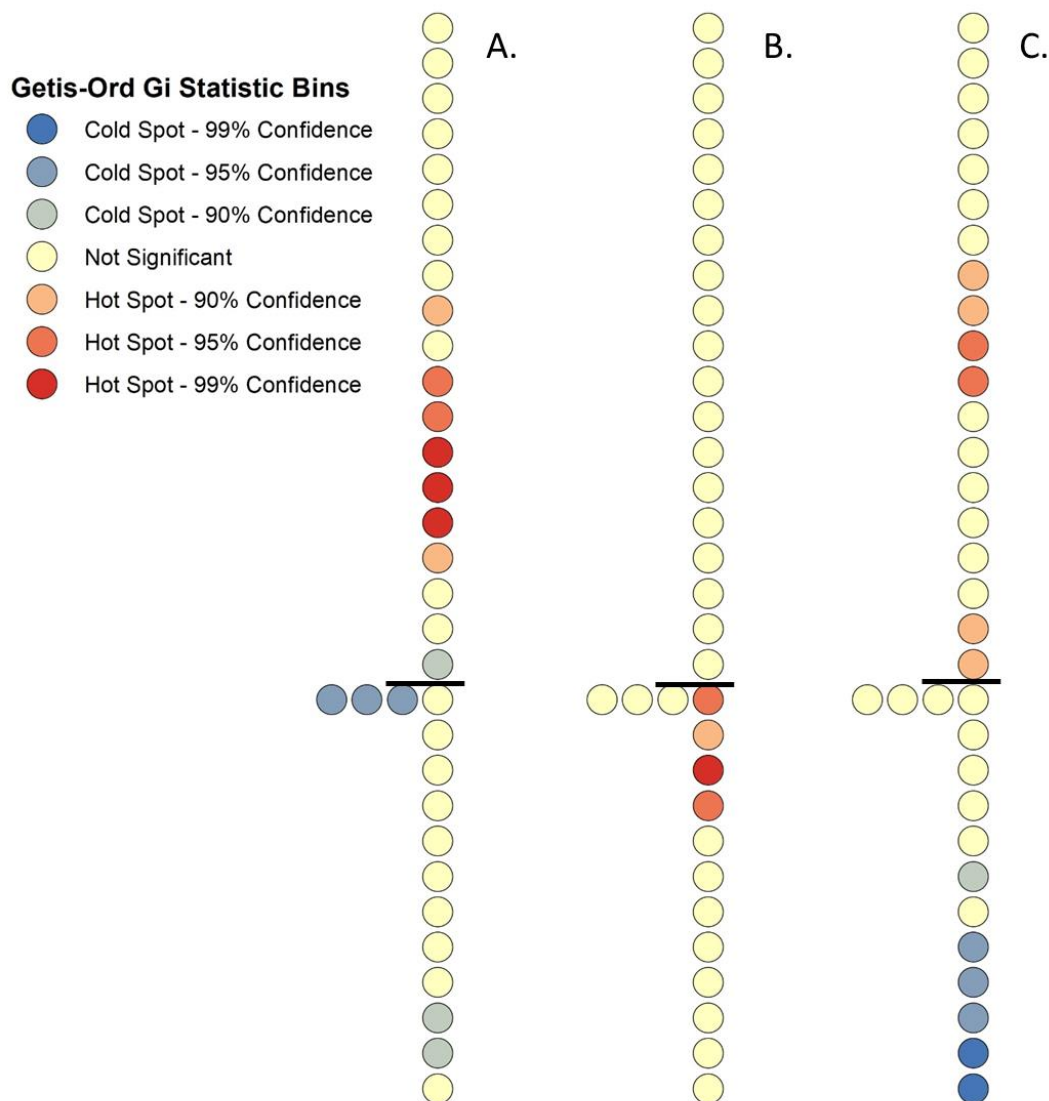


Figure 3.7: Getis-Ord General G spatial clustering of Rainbow Smelt density at 7 map units, (A.) 2015, (B.) 2016, (C.) 2017. The black bars denote the reservoir zone division.

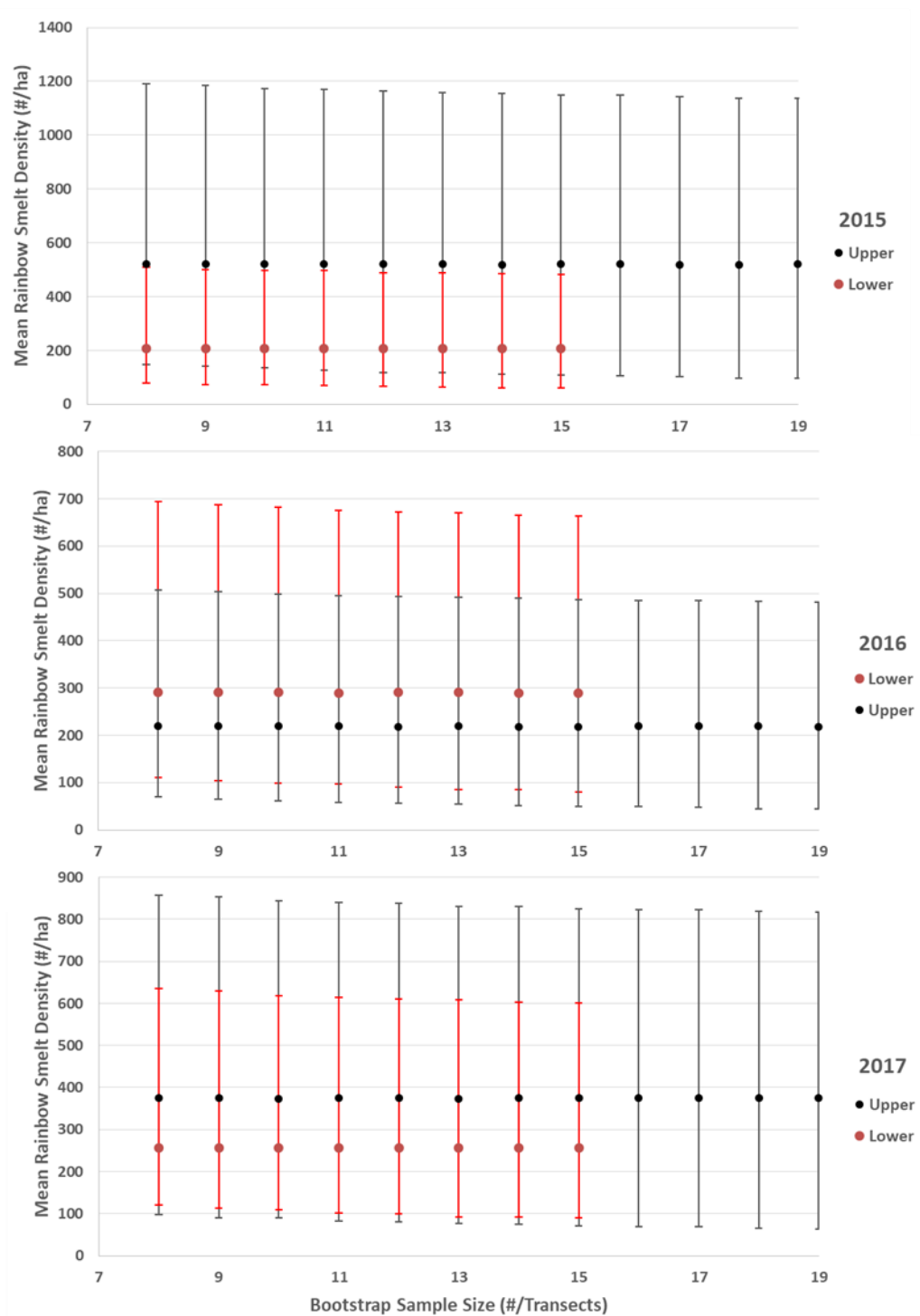


Figure 3.8: Bootstrapped estimates of upper and lower Lake Oahe mean Rainbow Smelt density (\pm 95% bootstrap percentile confidence interval).

Table 3.1: Getis-Ord General G spatial clustering results

	Year	Observed General G	Z- Score	p- value
7	2015	0.144	2.931	0.003
Map	2016	0.132	2.445	0.015
Units	2017	0.142	4.088	0.000
3.5	2015	0.072	2.375	0.018
Map	2016	0.068	2.607	0.009
Units	2017	0.708	6.552	0.000

Table 3.2: Estimated Rainbow Smelt sample sizes for upper and lower Lake Oahe ($\alpha =$

0.2). n = estimated sample size, CV = coefficient of variation of the sample.

		2015	2016	2017
Upper	n	8.152	9.469	7.195
Zone	CV	0.428	0.463	0.403
Lower	n	17.648	14.981	22.659
Zone	CV	0.625	0.576	0.708

CHAPTER 4: RAINBOW SMELT SPAWNING POPULATION AND HABITAT CHARACTERISTICS IN A MISSOURI RIVER RESERVOIR

Abstract

Rainbow Smelt *Osmerus mordax* are the primary coldwater forage species in Lake Oahe, South Dakota, yet most aspects of their life history remain mysterious. As Missouri River reservoirs present a novel habitat compared to elsewhere in the Rainbow Smelt's range, we investigated their spawning site use relative to physical and thermal habitat from spring 2016 – 2018 using a mobile horizontal-beaming hydroacoustic survey. We mapped spawning habitat using side-scanning sonar to establish relationships with site bathymetry and thermal spawning conditions. From our site mapping, we determined the depth, slope, bottom hardness, and ruggedness of individual sites. We used a PCA to condense our physical habitat metrics, with PC1 representing 77% of cumulative variance. Peak abundance was linked to this physical habitat gradient, representing [steep slope, deep, soft bottom] to [low slope, shallow, hard bottom]. Peak Rainbow Smelt spawning aggregations were observed at $6.8 \pm 1.7^{\circ}\text{C}$ (Mean \pm StDev). An information-theoretic regression analysis revealed an interactive effect of temperature and habitat, whereby shallower, warmer sites typically had a lower peak abundance. While challenges associated with horizontal hydroacoustic surveys remain, these results represent the first step toward understanding habitat use characteristics of spawning Rainbow Smelt in reservoir systems.

Introduction

Habitat plays a key role in the fisheries management process. While many of the abiotic factors affecting fish, such as seasonal weather patterns and temperature, are beyond managers' control, habitat can often be addressed. Fish habitat encompasses all of the physical and biological components of a system required to support fish growth, survival, and reproduction (Newcomb et al. 2007). More narrowly, the Magnuson-Stevens Act defines essential fish habitat as "those waters and substrates necessary to fish for spawning, breeding, feeding, or growth to maturity" (Magnuson-Stevens Act 2006). Thus, fish habitat encompasses all of the attributes of a system wherein a species is successfully completing its life cycle, with some locations within the system more essential for specific life stages.

If a species demonstrates a disproportionate use of a habitat type, it is inferred that selection has occurred for those habitat criteria (Krausman 1999). In practice, this inference is usually based on more observations or greater rates of occupancy for a given habitat type relative to alternatives. Proximate habitat selection is factor-based site selection of site attributes, whereas ultimate selection is based on outcomes such as reproductive success and survival (Hilden 1965). Cues for individual habitat use decisions are therefore the basis for eventual population outcomes. By extension, selection of spawning sites by adult fish should have consequences for the post-emergence offspring, and this in turn should have eventual population-level effects.

The concept of preferred spawning habitat is widely applied within fisheries, encompassing thermal and physical site attributes. Site selection varies widely by

species, as does overall spawning strategy. Winemiller and Rose (1991) classified a variety of North American fishes based on a trilateral gradient of fecundity, juvenile survivorship, and age of maturity in response to the spawning environment. Under their system, opportunistic species are typified by early maturation, frequent reproduction over an extended spawning season, rapid larval growth, and rapid population turnover. The opportunistic spawning strategy's success hinges on maximizing colonization across environments with frequent, stochastic change on relatively small spatial and temporal scales. Thus, it would be expected that spawning site selection plays a relatively small role for these species. Conversely, periodic species are typified by delaying maturation to attain a larger adult size, increasing survival and producing larger clutches. Periodic species also exhibit synchronous spawning episodes, whereby movement into preferred spawning habitat or a favorable spawn timing (e.g. spring) is expected.

Rainbow Smelt *Osmerus mordax* represent an intermediate strategy. They are a small bodied, relatively short lived species with seasonal spawning, moderately large clutches, small eggs, and only a few spawning bouts per season (Winemiller and Rose 1991). Although Rainbow Smelt exhibit iteroparity and recurrent annual site use (Murawski et al. 1980) throughout range, Lake Oahe, South Dakota represents a novel habitat as a large prairie reservoir. Rainbow Smelt have been present since the early 1970's, and are the dominant forage species for Walleye *Sander vitreus*, the primary sport fish in the system. Although the importance of the species is well-documented, relatively little is known about the Lake Oahe Rainbow Smelt spawn timing, site selection, or spawning stock attributes. Additionally, Rainbow Smelt abundances in Lake

Oahe are variable through time. It would therefore be beneficial to understand how reservoir habitat and spring conditions influence Rainbow Smelt spawning, as this would aid in predicting future trends within the Walleye forage base. We therefore 1) documented Rainbow Smelt spawning abundances across the reservoir to determine spatial patterns of spawning occurrence, 2) mapped the spawning sites to determine if bathymetric habitat features indicated site selection patterns, and 3) incorporated spring warming patterns to evaluate how temperature mediates the Rainbow Smelt spawning-habitat relationship.

Methods

Study area – Lake Oahe is the second largest storage reservoir on the Missouri River, stretching 372 km from central North Dakota to central South Dakota (Figure 4.1). At normal pool, Lake Oahe's surface area measures 145,000 ha, with 3,623 km of shoreline. Three major tributary arms, along with myriad embayments, provide complex littoral habitats, with an overall shoreline development index of 27.4 (Nelson and Walburg 1977). The upper portion of Lake Oahe in South Dakota is mesotrophic, and transitions to oligotrophic downstream toward the dam (Finzel 2011). The lower 169 km of Lake Oahe, approximately 68,500 ha, annually stratify during the summer months (Burczynski et al. 1987), and support a 2-tier fishery. Although Rainbow Smelt spatial distribution is constrained by thermal habitat during this period, temperature conditions following ice-out allow Rainbow Smelt access to the entire reservoir.

Rainbow Smelt were first detected in Lake Oahe in 1972, following a 1971 stocking by North Dakota Game and Fish in Lake Sakakawea, 165 km upstream of Lake

Oahe. Before the 2011 Missouri River flood and attendant Rainbow Smelt population crash (Fincel et al. 2016), a short-term spring recreational Rainbow Smelt dip net and seine fishery existed at most public access locations on the eastern shore of Lake Oahe (Robert Hanten, SDGFP, personal communication). These anecdotes represented a variety of potential spawning habitats across a 155 km latitudinal gradient, and formed the basis for our sampling spatial and temporal frame.

Spawning survey and analysis – Due to the large spatial extent of our sampling frame, we favored complete spatial coverage over complete replication. We surveyed 32 sites, organized as 7 lake regions (Figure 4.1), within an incomplete design during the springs of 2016-2018, using “region” and “year” as blocking variables. Regions were designed to cover the entire longitudinal extent of the reservoir with roughly equidistant spacing. Each region was randomly assigned 2 survey springs and 1 excluded spring. Each spring consisted of 3 survey periods, with 7-10 days (weather dependent) between visits to a region. Within a region, each site was a 1 km transect, transects apportioned evenly between embayment and reef/point habitat types. Each region contained 4 – 6 sites, with a minimum of 2 km between sites. We randomized transect sampling order upon each regional visit to avoid systematic temporal biases. We utilized this design to maximize our spatial coverage of Lake Oahe, while still providing site replication through the spawning period following ice-out.

We utilized a mobile horizontal-beaming hydroacoustic survey to determine the abundance of Rainbow Smelt at each site. While this method did not actually observe Rainbow Smelt in the act of spawning, we assumed the hydroacoustic estimate of each

transect represented a snapshot of spawning Rainbow Smelt abundance at a given site and time. Surveys commenced 30 minutes after sundown, and were run in darkness with only running lights on the survey vessel, given the documented light avoidance of spawning Rainbow Smelt (McKenzie 1965). Hydroacoustic surveys were conducted using a Biosonics DT-X system with a 420 kHz split beam transducer. The transducer had a 6.9° circular beam, and was mounted at a 4° angle below horizontal to avoid surface interference during choppy conditions (Gangle and Whaley 2004). Survey settings were 5 pings/s with a pulse duration of 0.5 ms, with a -100 dB collection threshold. System calibration was periodically checked according to the manufacturer's instructions using a 17.5 mm tungsten carbide target sphere and the apparatus described by Foote et al. (1987). Echogram creation used 40-log(R) time varied gain, 3 dB 1-way maximum gain compensation, and echo length 0.80 – 1.20 times the original pulse length, using Sonar5-Pro (Balk and Lindem 2015). We utilized the Sonar5-Pro cross-filter detector optimized for fish tracking to extract individual fish tracks from the echogram. The cross-filter detection method is based on 2-dimensional low-pass filters, advancing the image processing analysis approach (Balk and Lindem 2000), and is demonstrated in detail in Balk and Lindem (2002). To convert target strength (TS) to approximate fish length and subsequently assign a species identification, we used the TS equation developed at 420 kHz for horizontal Rainbow Trout *Oncorhynchus mykiss* from Kubecka and Duncan (1998), expressed in the general form of Love (1977):

$$TS = 27.48 * \log_{10}(10 * TL) - 98.6$$

where TS is the target strength of an individual fish, and TL is the total length (cm) of the fish. This equation is very similar to the Kubecka and Duncan (1998) mixed stock 420 kHz equation; however, we use the Rainbow Trout TS -equation because both species have a physostomous swim bladder and are phylogenetically close (Betancur et al. 2013).

Hydroacoustics, when employed alone, cannot determine species composition. An additional sampling technique is necessary to generate length-frequencies of species present at the time of the hydroacoustic survey. We accomplished this using 9.5mm mesh, 1.2 x 30.5 m monofilament gill nets (0.12 mm diameter), fished as short term benthic sets while we conducted the hydroacoustic survey. Nets were oriented perpendicular to the shoreline at 2-3 m depth. Captured Rainbow Smelt were sexed and total length was recorded. All captured individuals were expressing gametes, regardless of sex. Lengths were also taken from any bycatch. These were examined for percent overlap in length-frequency distribution with Rainbow Smelt for length-based assignment of species identification, similar to Fincel et al. (2016).

A random subsample of Rainbow Smelt ($n = 211$) was retained for age-length analysis in 2018. The sagittal otoliths of these fish were mounted in epoxy (Buehler, EpoxiCure 2, Lake Bluff, Illinois), cross sectioned using a low speed isometric saw (Buehler, M11-1280-160, Lake Bluff, Illinois), and photographed under an Olympus SZX 16 dissecting microscope. Otoliths images were then consensus aged using three readers (Quist and Isermann 2017), and a von Bertalanffy growth curve was fit using the least-squares method.

Habitat survey and summary – We developed explanatory habitat metrics for spawning Rainbow Smelt abundances. We recorded visit-specific thermal conditions by calculating the mean of a temperature profile at the centroid of each hydroacoustic transect, excluding the 1 m surface layer. We used site-specific variables to describe the bathymetry and bottom habitat attributes. We refer to this as physical habitat hereafter. To generate these spatial variables, we mapped all our sites in 2018 using a Lowrance HDS 7 unit with 200kHz HDI transducer. Three mapping transects were laid out parallel to shore using 2018 TerraColor Landsat 8 aerial imagery mosaics (Earthstar Geographics 2018). The outermost transect was at 50m, and the innermost was as reasonably close to the shoreline as could be accomplished without running aground. The middle transect was 25m from shore, with occasional deviations to cover bathymetric features of interest (e.g. prominent reef). Transects were mapped at maximum 8 kmph, and slowed depending on wave interference and real-time visual assessment of sonar performance. Although we acknowledge water levels are dynamic in reservoirs and actual wetted shoreline may have fluctuated inter-annually, we assumed our 2018 mapping data was representative of the habitat available at each site.

Post-processing was completed by BioBase (2018). Output was 2D point cloud with depth, slope, and bottom hardness attributes, encompassing the shoreline along the 1 km hydroacoustic transects and extending 50 m offshore. The point cloud was subsequently rasterized, following recommendations from BioBase (2018) using the Feature to Raster tool in ArcGIS 10.4 (ESRI 2016). From this, we calculated the vector

ruggedness measure (VRM), which measures terrain ruggedness as the variation of 3D orientation in neighborhood cells, condensing slope and aspect variance into a single measure. This is scaled from 0 (no terrain variation) to 1 (complete variation), with typical ranges between 0-0.4 (Sappington et al. 2007). We applied this terrestrial metric as an index of bathymetric habitat complexity, and favored it over other options because it is less correlated to slope as other derived ruggedness metrics (Sappington et al. 2007). We used mean values for site habitat variables to simplify analysis.

We then condensed the habitat variables into a single descriptive metric using a principle components analysis (PCA) in R (R Core Team 2018) using the “stats” package (R Core Team 2019) to minimize collinearity concerns for further analyses. We checked the data for normality using normal QQ-plots, and assessed collinearity with Pearson’s correlation tests. As expected, all habitat metrics were significantly collinear ($p < 0.05$). Despite this, we included VRM, depth, slope, and bottom hardness in the PCA, and examined the component loadings. The first and second components included the same two variables, and were biologically relevant. We therefore retained the first component as an independent variable describing a physical habitat gradient, and reference this variable as PC1.

Other Statistical Analysis – We compared Rainbow Smelt spawning abundances, our dependent variable, to the PC1 habitat gradient, mean temperature, and the date of the survey. We used Pearson’s correlation tests to explore relationships between the independent variables. As temperature and date were collinear, we only used temperature in the following analysis. We used an information theoretic multiple

regression analysis to determine the nature of the temperature-habitat interaction on peak spawning abundance, and how that relationship changed throughout the spring warming period. This was conducted with all peak abundances pooled using the R package “AICcmodavg” (Mazerolle 2019).

Results

Spawning surveys –Rainbow Smelt length-frequency distribution did not overlap with bycatch species in the gillnet data (Figure 4.2). This result was consistent for 2016, 2017, and 2018. Rainbow Smelt typically were between 105 and 155 mm, with the occasional 160 mm fish. Bycatch species included Yellow Perch, Spottail Shiner, Walleye, and immediately post-stocked Chinook Salmon, but the percent overlap of these species with the Rainbow Smelt length-frequency distribution was minimal (Figure 4.2, Table 4.1). We therefore were confident that any fish within the aforementioned size range was a Rainbow Smelt.

Rainbow Smelt spawning distributions, as detected by our hydroacoustic survey, varied widely between survey years (Figure 4.3). In 2016, the highest spawning abundances were in the Cheyenne River arm, with another concentration at Whitlock’s Bay. By comparison, abundances in the Spring Creek and Moreau River/Swan Creek regions were intermediate. The Mobridge region recorded the lowest abundances. In 2017, Whitlock’s Bay again recorded high abundances, comparable to the 2016 estimate; however, the highest abundances were in the Mobridge area, contrary to the 2016 pattern. The Bush’s Landing region, immediately south of Whitlock’s Bay, had low abundances, with the lowest in the Pollock/Shaw Creek region, at the northernmost

extent of the survey area. In 2018, the Spring Creek region unexpectedly recorded the highest abundances. The Cheyenne River, highest in 2016, was intermediate, along with the Moreau region. Bush's Landing was again low, comparable to 2017, with the lowest abundances again in the Pollock/Shaw Creek area. We were unable to detect any consistent "hot spots" of Rainbow Smelt spawning abundance. Instead, we discovered widespread use of the reservoir for spawning activity. The exception to this was the Pollock region, where Rainbow Smelt abundances were consistently low to nonexistent.

From the 2018 subsample, the age structure of spawning Rainbow Smelt was dominated by age-3 fish (54%, Figure 4.4). Age-4 fish were the next most numerous (25%), followed by age-2 (11%), age-5 (8%), and age-6 (2%). Overall, the Rainbow Smelt spawning population is generally comprised of younger fish, which is not uncommon for prey species. We recorded mature, spawning age-2 females and males. No age-1 Rainbow Smelt were sampled. Rainbow Smelt growth was asymptotic (Figure 4.4), with a small increase in mean length-at-age between ages 2 and 3 (9 mm), and little growth occurring after age-3. This age and size structure is consistent with Rainbow Smelt sampled by SDGFP over the preceding two decades (e.g. Lott et al. 1994, Johnson and Riis 1995, Johnson et al. 1997, Adams et al. 2009, Longhenry et al. 2010, Potter et al. 2016).

Peak abundances detected at sites varied by survey period (Figure 4.3), and we used temperature and date to examine this pattern. Peak abundances occurred in the water temperature range of 5 - 9°C during 2016 and 2017 (Figure 4.5). An abnormally late ice-out occurred in 2018. Peak abundances were observed at higher temperatures

than 2016 or 2017, with some peaks at comparable low temperatures. The 2018 peak abundances occurred 2 – 4 weeks later (Figure 4.6), which lead to a wider temperature range than previous years (Figure 4.7). The wider range of temperatures is due to differential warming rates across the large north-south extent of Lake Oahe, in addition to complex reservoir morphology. In the “normal” years, assuming 2018 to be abnormal, Rainbow Smelt spawning peaked approximately mid-April and was concluding near the first week of May.

Although temperature plays a major role in Rainbow Smelt spawn timing, we also investigated the influence of physical habitat on the variable spawning Rainbow Smelt abundances. To condense the environmental variables generated from our site mapping, we conducted a PCA. The loadings for the first 2 components accounted for 99% of the variance, and the components contained the same 2 variables (Table 4.2). The first component's scores (PC1) were used as a predictor variable. Higher PC1 scores were correlated to deeper, steeper, softer-bottom sites, while low PC1 scores described shallow, low slope, hard bottom sites.

The information-theoretic regression approach related the PC1 habitat metric and mean site temperature to peak observed spawning abundance. We modelled the relationship as 2 simple linear regressions and 2 multiple regressions, 1 additive and 1 multiplicative interaction, because we were curious of the nature of the interaction, if any existed (Table 4.3). The two interaction models described the data well ($\Sigma \text{AICc } W = 0.56$), although it was evident from the single term models that temperature ($\text{AICc } W = 0.26$) independently was more influential than habitat ($\text{AICc } W = 0.06$). Overall,

temperature ($\Sigma AICc W = 0.82$) had stronger support than habitat ($\Sigma AICc W = 0.62$), yet the top interaction model was separated from the habitat model by $\Delta AICc = 3.70$. All biological models outperformed the intercept model (Table 4.3).

We used the top model, with the multiplicative interaction, to examine how temperature and habitat interacted with peak spawning abundances. To visualize how this interaction changes through the spring, we used the minimum, 1st quartile (Q1), median, 3rd quartile (Q3), and maximum temperatures. At the minimum temperature, Rainbow Smelt displayed a weak affinity for shallower sites (Figure 4.8). As temperatures warmed into the Q1 and median ranges, where the highest peak abundances were observed (5.8 – 6.8°C, Figure 4.5), Rainbow Smelt spawning site abundances became more associated with deeper, steeper sites (Figure 4.8). The relationship between higher abundances and deeper, steeper habitat became progressively more pronounced at the upper end of the temperature range (Q3 and maximum, Figure 4.8).

Discussion

We observed a habitat preference for spawning Rainbow Smelt mediated by thermal conditions. Thermal influences on Rainbow Smelt spawn timing have been documented in Maine inland lakes (Rupp 1959), Lake Champlain (Simonin et al. 2016), and the Great Lakes region (Creaser 1925, O'Brien et al. 2012), with spawning taking place shortly after ice out. Lake Oahe peak abundances were generally recorded between 5-9°C, with sampling occurring across a temperature range from 3.5°C upward to 17°C. The thermal range of peak detections is similar to that of O'Brien et al. (3-10°C,

2012) in Lake Huron tributaries, and the stream (4.5-7°C) and Great Lakes (2.2-14.5°C) ranges from Carlander (1969). As our observations spanned a wide range of dates due to a late spring in 2018, Rainbow Smelt tend to be more temperature-oriented than photoperiod-oriented on the gradient described by Winemiller and Rose (1991).

Deeper, steeper habitats were generally preferred as temperature increased. Given the role of temperature cues in Rainbow Smelt spawning, access to deeper thermal refuges seemed to increase in importance as spring warming progressed. In the Great Bay and Piscataqua estuary system, NH, Rainbow Smelt visited multiple rivers during the spawning season, and retreated to the deeper waters of the estuary and near-coast between spawning bouts and after conclusion of spawning (Enterline 2013). As 15°C is generally when spawning ceases (Carlander 1969, Scott and Crossman 1973), the use of sites near deep thermal refuges may allow spawning to continue where the inshore temperature is at or near the maximum temperature threshold.

We did not observe a relationship with bottom hardness, a proxy variable for composition, and spawning adult abundance. Our sampling incorporated a variety of embayments, the number and diversity of which are the defining feature of the Lake Oahe shoreline (Figure 4.3). Rainbow Smelt have been observed spawning on fine sand, boulders, mud, aquatic vegetation, brush, flooded grassland, concrete, and wooden sluiceways (Rupp 1959), with sand and gravel usually considered ideal (Scott and Crossman 1973). A diversity of spawning substrates is not unusual for broadcast spawning species; however, eggs spawned on a diversity of substrates do not survive at similar rates. On the preferred substrates, egg suffocation was not identified as major

cause of mortality; instead, wave action was the primary cause of Rainbow Smelt egg mortality, with more exposed sites experiencing higher mortality (Rupp 1965). While silt-egg interactions were not explored in Rainbow Smelt, 2 mm of silt coverage is sufficient to cause 71% Walleye egg mortality, which are another lithophilic broadcast spawner (Gatch et al. 2019). Thus, we assume silt substrates would be less optimal for Rainbow Smelt egg survival, but locations may not be actively selected against by spawning adults. At the rear of many Lake Oahe embayments are creeks and we reasoned these lotic habitats were not likely responsible for major annual reproductive contributions due to excessive sediment. Each of the major western tributaries of Lake Oahe contribute massive volumes of sediment per year to the reservoir: the Grand (970,905 tons/year), Moreau (1,431,475 tons/year), and Cheyenne Rivers (5,459,641 tons/year, USDA NRCS 2009). Creaser (1925) noted the spawning Rainbow Smelt is not a strong swimmer and does not ascend far upstream. Rainbow Smelt in streams deposit eggs across the full gradient of stream habitat available as one works upstream (Creaser 1925). In the case of Lake Oahe, such a gradient equates to tributary channels with accumulated clay silts that stretch for several river miles upstream. Rainbow Smelt preferred stream spawning habitat includes riffles with larger diameter substrate (10-20 cm, Chase 2006), or clean gravel and coarse sand (Scott and Crossman 1973). High turbidity causes cessation of Rainbow Smelt spawning (Murawski et al. 1980). Thus, we qualitatively judged the sediment impaired, low gradient stream habitat local to the reservoir, which is quite turbid during spring runoff, to be generally unsuitable for spawning runs of Rainbow Smelt. Although some stream spawning may occur given the

behavioral plasticity of Rainbow Smelt, we believe the Lake Oahe population to be dominated by shore spawning.

Accordingly, we concentrated on Rainbow Smelt spawning on lake shorelines and reefs. Although stream spawning is common across the Rainbow Smelt range (Scott and Crossman 1973), lake spawning can sustain populations in the absence of suitable stream habitat (Rupp 1959). Lake spawning can also provide more consistent production, as seen in St. Martin Bay, Lake Ontario, where lake-contribution larva were moderate, yet less variable relative to streams (Brown 1994). In Lake Oahe, lake spawning Rainbow Smelt site abundances were inconsistent between survey periods and years (Figure 4.3). Although recurrent stream site use is common elsewhere in the Rainbow Smelt range (Murawski et al. 1980), it appears our lake spawning population lacks a reliable spatial pattern.

This would seem to indicate that on the Winemiller and Rose (1991) gradient of photoperiod vs. temperature spawning cues, temperature is the more dominant factor driving the Lake Oahe Rainbow Smelt spawn timing. The unusually late spring ice-out in 2018 led to peak Rainbow Smelt spawning abundances observed over two weeks later than the preceding two years. Were photoperiod the dominant cue, we would expect to see a lower magnitude of peak spawning activity, with the peak occurring under the ice and before surveying commenced. Under ice spawning does occur (Rupp 1959, Carlander 1969), but peak activity is generally after ice out at slightly higher temperatures (Rupp 1959, Creaser 1925, O'Brien et al. 2012). It may be that Rainbow Smelt stage inconsistently throughout the reservoir and have spawning movements at

various locations, cued by temperature. This is consistent with estuarine Rainbow Smelt spawning movements, where male and female fish visited multiple rivers within a coastal embayment in a single spawning season (Enterline 2013, Murawski et al. 1980).

The aging subsample was dominated by 79.6% male fish. The nearly 4:1 sex ratio (M:F) is not unexpected for Rainbow Smelt sampled during the spawn, as there is ample evidence that males generally spend more time at the spawning grounds than females (Rupp 1968, McKenzie 1964), with sex ratios in excess of 8:1 reported (Murawski et al. 1980). Repeat spawning bouts are observed in males and females, but males made spawning movements at 1.6 - 3.7 times the frequency of females (Enterline 2013). Our sample was therefore consistent with those reported elsewhere.

The Lake Oahe Rainbow Smelt age and length distributions were skewed toward older and smaller individuals. In Lake Oahe, length was asymptotic and little difference was observed between lengths at age for smelt 2-6 years old. Overall Lake Oahe mean length (120.7 ± 11.5 SD) was approximately 25 mm less than Gulf of Maine age-1 Rainbow Smelt (Enterline 2013). This is also smaller than the 178-203 mm average adult size reported by Scott and Crossman (1973). Lake Oahe Rainbow Smelt lengths were consistently below the range-wide length-at-age data from Carlander (1969), with average length-at-age smaller than the dwarf race of Rainbow Smelt reported from Lake Champlain and inland Atlantic Northeast lakes (mean = 157 mm, age-3). Size appears to be genetically plastic, as shown by anecdotes of transplantation experiments from dwarf Rainbow Smelt source populations (Carlander 1969). Our population follows the trend of small, inland systems having smaller mean adult lengths (mean = 104 mm) than

larger-bodied marine or Great Lakes populations (up to 356 mm, Scott and Crossman 1973), despite the large scale of Lake Oahe. Our sampled age distribution is probably the result of late maturation. Rainbow Smelt typically mature at ages 2-3 (Carlander 1969), yet a majority of our sample of actively spawning fish was comprised of individuals \geq age-3.

The slow growth of Lake Oahe Rainbow Smelt, and possibly the resultant delayed maturation, may be diet related. Rainbow Smelt are usually zooplanktivorous as juveniles, transitioning to piscivory with increasing size (Carlander 1969). Yet, in a survey of adult Rainbow Smelt diets in Lake Oahe, fish occurred in diets with a frequency of 0.7%, with Chesson's selectivity values of nearly 0, which is below neutral selectivity levels (Karnitz 1992). A decade later, stable isotope analysis showed that Rainbow Smelt adults remained partially zooplanktivorous, roughly one trophic level below Walleye, a top-tier piscivore in Lake Oahe (Davis 2004). The dominance of zooplankton diets, and the incomplete piscivory of Lake Oahe Rainbow Smelt may explain their slow growth, as the energy density of invertebrates is less than fish (Karnitz 1992, Davis 2004). Rainbow Smelt diets in Horsetooth Reservoir, CO (755 ha), were similar and yielded similarly depressed adults size structure, despite the differences in system scale (Johnson and Goettl 1999). The exact cause of the small adult size structure in Lake Oahe, however, remains unknown.

Our survey and analysis did make some important assumptions. The use of the Kubecka and Duncan's (1998) Rainbow Trout 420 kHz horizontal beaming TS-equation coefficients likely affected our *in-situ* length estimates, as species- and frequency-

specific equations are generally preferable (Simmonds and MacLennan 2005). Despite the widely acknowledged concerns with generalized TS-equations (Simmonds and MacLennan 2005), these equations, notably Love (1977), continue to be used (e.g. Fincel et al. 2016). Additionally, the generalized use of Rainbow Trout equations for the pelagic fish community has demonstrated utility and precedent (Yule 2000). We also may not have observed all spawning Rainbow Smelt directly, as some spawn in waters ≤ 0.5 m (Rupp 1959, Rupp 1965), which is beyond the reach of horizontal beaming sonar. Instead, we likely observed fish spawning in slightly deeper water offshore, similar to Nellbring (1989) and Evans and Loftus (1987), or staging prior to inshore movement. If we hydroacoustically counted Rainbow Smelt at a given transect, we assumed that fish was spawning immediately inshore from its location or within the 0.5 km transect, as that was inference scale. Given the propensity of males to remain on the spawning ground awaiting females, out of our detection ability, we may have scanned a disproportionate number of staging females, which would only serve to strengthen the importance of the deeper, steeper sites that seemed preferable.

Management Implications

Presently, Lake Oahe water level management is conducted by the US Army Corps of Engineers, with recommendations by SDGFP to favor spring reservoir surface elevations remaining steady or rising. The goal, among others, was to prevent egg stranding from occurring on shallow, sandy flats, where Rainbow Smelt have been detected in the past with a combination of seines and mini-fyke nets (South Dakota Game, Fish and Parks, unpublished data). This recommendation also protects Rainbow

Smelt eggs spawned along the shoreline of steeper sites, which we observed to be important. Subsequently, we suggest SDGFP continue recommending stable to rising reservoir surface elevations.

Conversely, we hoped to identify a spawning habitat niche for Rainbow Smelt that could be replicated over time around the reservoir to enhance the overall quantity of spawning habitat available. This proved to be elusive, as firm habitat correlations did not exist beyond general slope and depth metrics. Instead, Rainbow Smelt spawning occurs in indeterminate locations throughout the reservoir that meet general thermal criteria, attenuated by bathymetry throughout the spring warming period.

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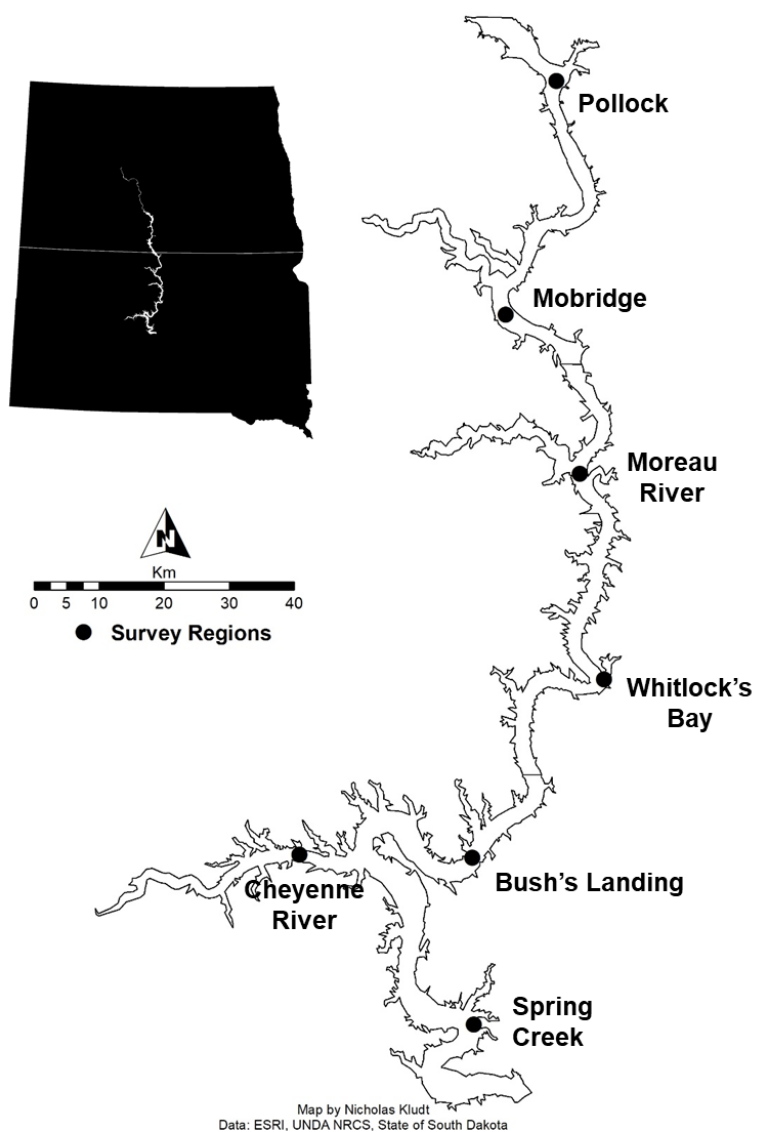


Figure 4.1: Spring hydroacoustic survey regions, 2016-2018, in Lake Oahe. Inset – Lake Oahe location in North and South Dakota.

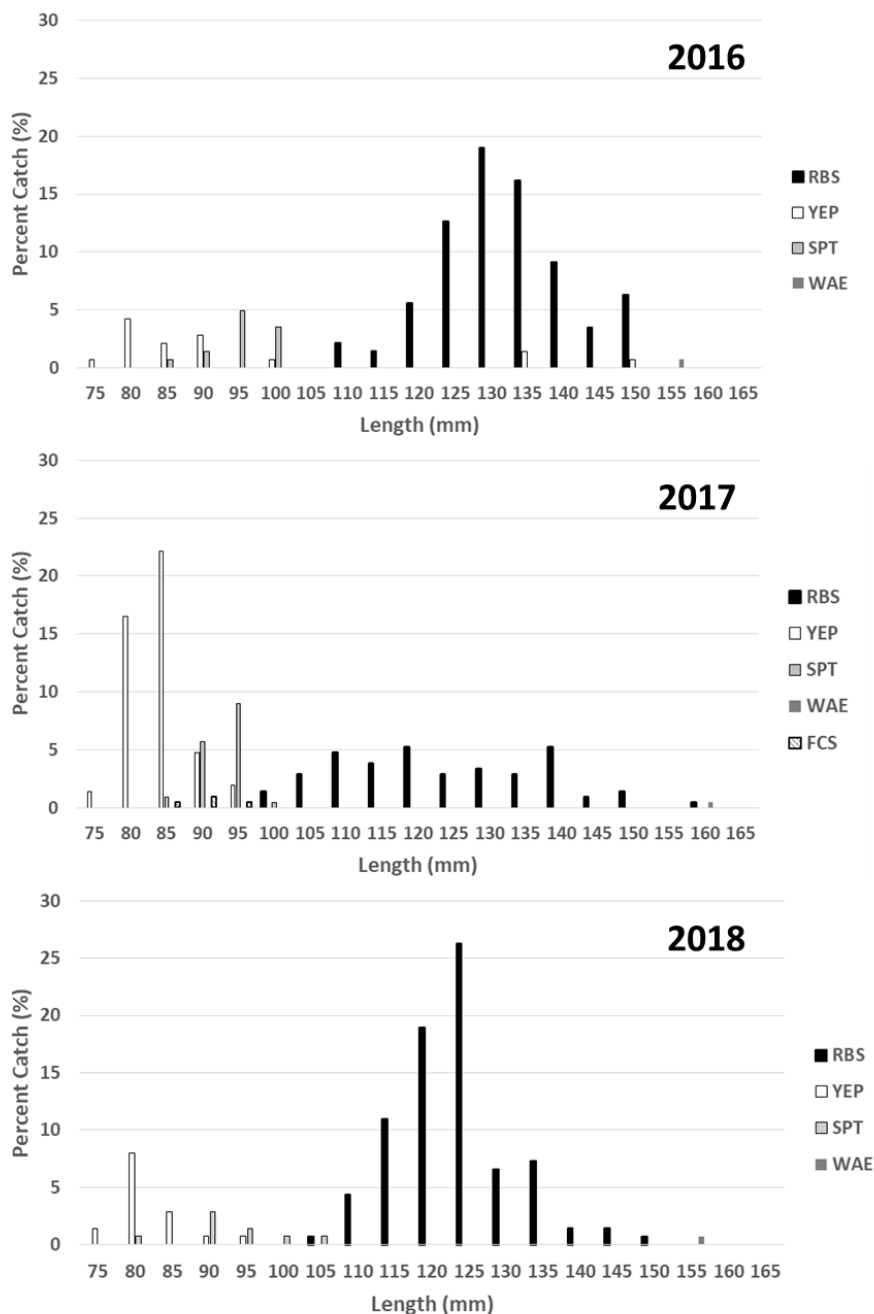


Figure 4.2: Length-frequency distribution of Rainbow Smelt and bycatch species by 5 mm length bin from short term gillnetting, 2016-2018, Lake Oahe, South Dakota. RBS – Rainbow Smelt, YEP – Yellow Perch, SPT – Spottail Shiner, WAE – Walleye, and FCS – Chinook Salmon.

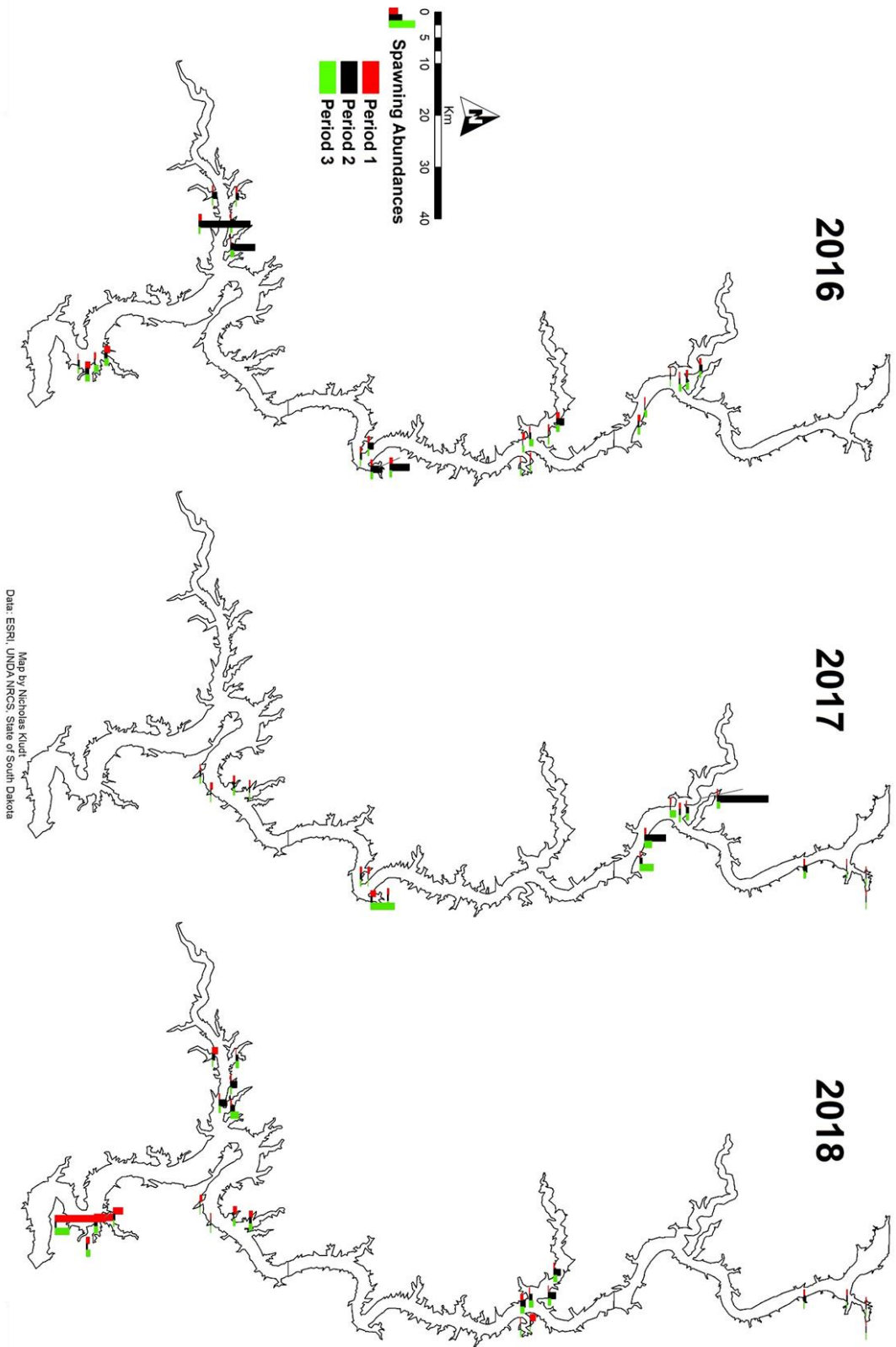


Figure 4.3: Rainbow Smelt spawning abundances by survey period, 2016-2018, Lake Oahe, South Dakota.

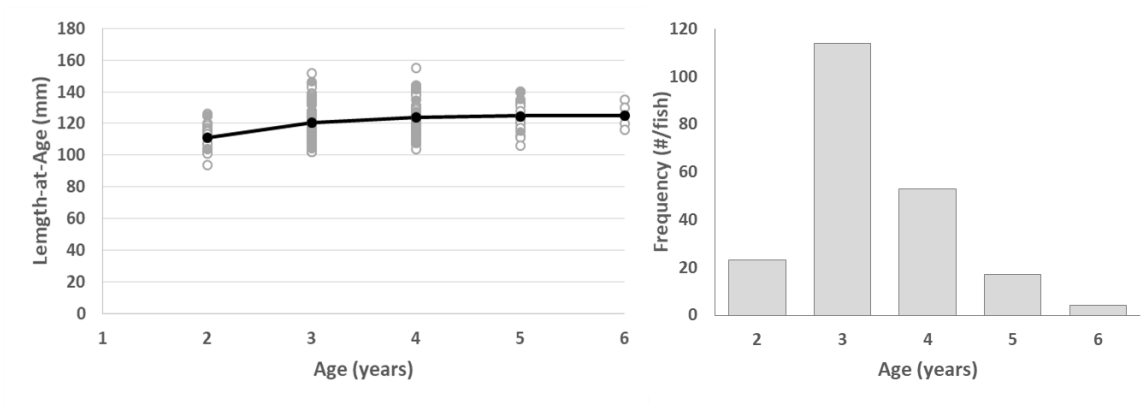


Figure 4.4: Von Bertalanffy growth model for spawning Rainbow Smelt mean length-at-age, 2018 (Left), and age frequencies (right), Lake Oahe, South Dakota. Regression parameters: $L_{\infty} = 125.25$, $k = 1.10$, $t_0 = 0.025$, $r^2 = 0.99$. Female (dark grey, $n = 43$), male (hollow, $n = 168$), and estimated mean (black) lengths shown for reference.

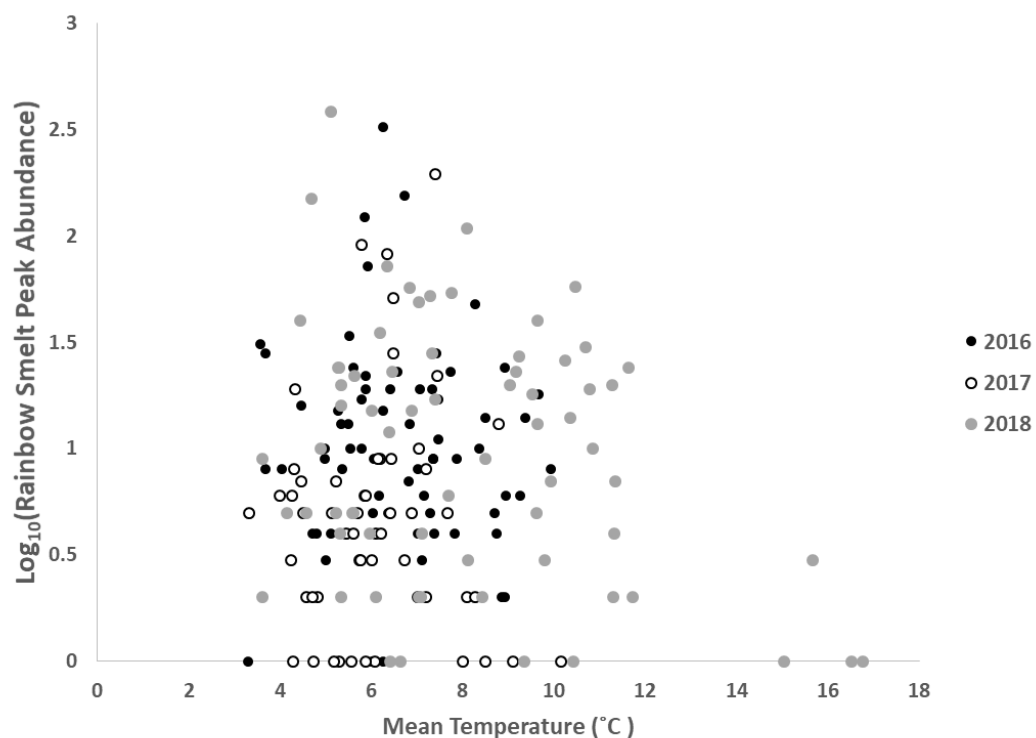


Figure 4.5: Transformed peak Rainbow Smelt site detections, 2016-2018, by mean site temperature, determined from a profile taken at the transect centroid, Lake Oahe, South Dakota. Mean temperature excludes 1 m surface layer.

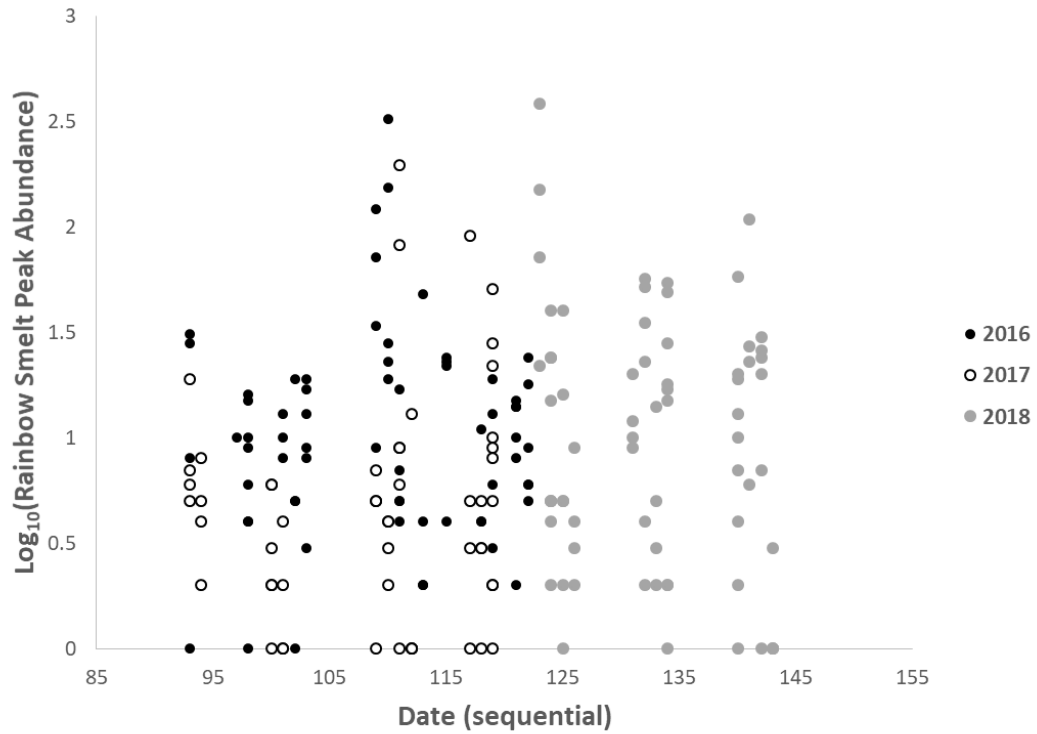


Figure 4.6: Transformed peak Rainbow Smelt site detections, 2016-2018, by date, Lake Oahe, South Dakota. Sequential days start January 1 and include 2016 leap day.

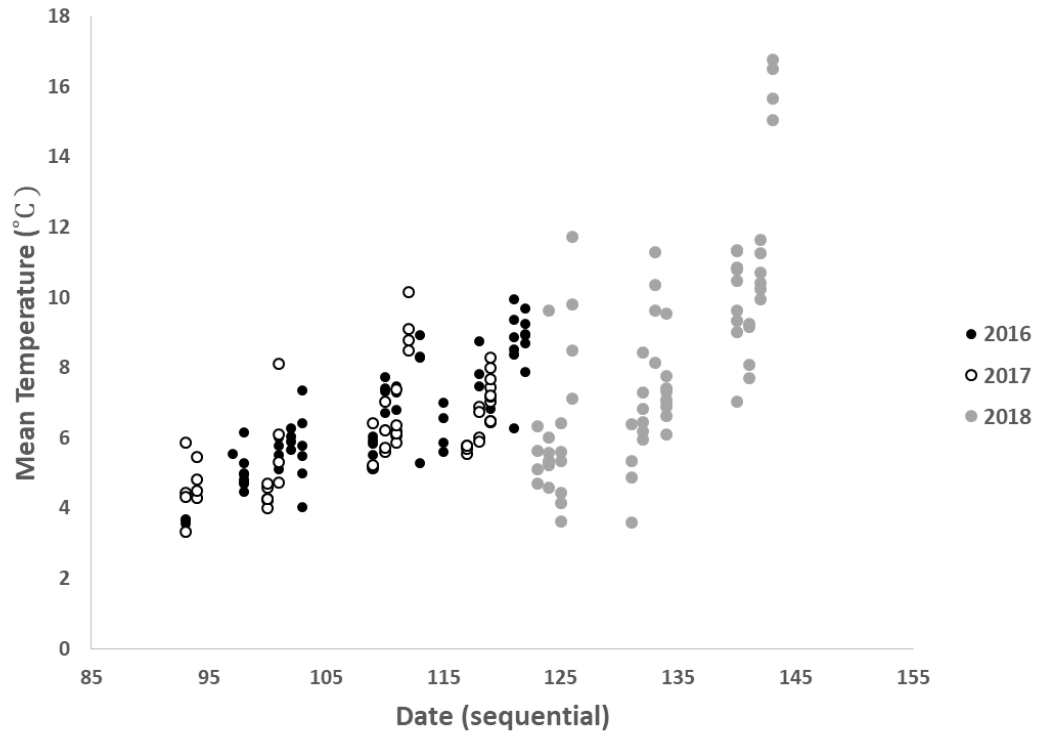


Figure 4.7: Spring warming patterns, 2016-2018, Lake Oahe, South Dakota. Mean site temperature was determined from a profile taken at the transect centroid, excluding the 1 m surface layer. Sequential days start January 1 and include 2016 leap day.

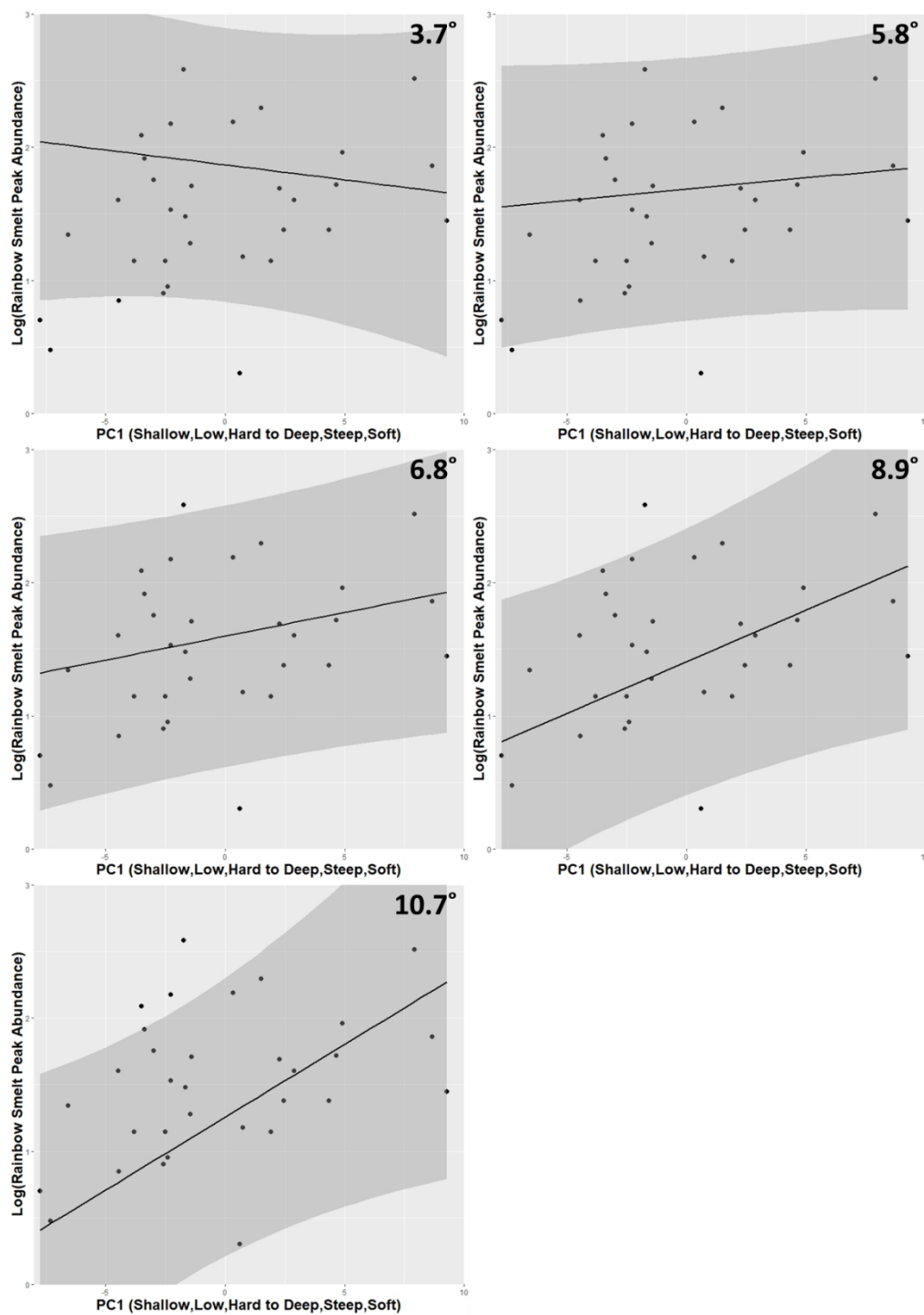


Figure 4.8: Multiple regression of Rainbow Smelt \log_{10} - transformed peak abundance by PC1 habitat gradient and temperature. Temperature values (L to R) represent minimum, quartile 1, median, quartile 3, and maximum site temperatures.

Table 4.1: Annual Rainbow Smelt % length-frequency overlap with bycatch species and total % overlap from short term gillnetting, 2016-2018, Lake Oahe, South Dakota. RBS – Rainbow Smelt, YEP – Yellow Perch, SPT – Spottail Shiner, WAE – Walleye, FCS – Chinook Salmon.

Year	YEP	SPT	WAE	FCS	Total
2016	2.11	0.00	0.00	0.00	2.11
2017	0.00	0.47	0.47	0.00	0.94
2018	0.00	0.73	0.00	0.00	0.73

Table 4.2: Principle components analysis results of physical habitat variables. PC1 values, retained for analysis, represent a gradient, with higher values indicating a steeper, deeper, softer bottomed site.

	Comp. 1	Comp. 2
Standard Deviation	5.1167	2.754
Cumulative % Variance	0.779	0.999
Loadings:		
Mean VRM	-	-
Mean Depth	-0.832	0.555
Mean Slope	0.555	0.832
Mean Hardness	-	-

Table 4.3: Information theoretic multiple regression results of Rainbow Smelt abundance compared to habitat covariates.

Model	k	$\Delta AICc$	AICc <i>W</i>
Temp * Habitat	5	0.00	0.39
Temp + Habitat	4	0.76	0.27
Temp	3	0.77	0.26
Habitat	3	3.70	0.06
Intercept	2	6.08	0.02

CHAPTER 5: EVALUATING RAINBOW SMELT LARVAL DYNAMICS IN MISSOURI RIVER RESERVOIR HABITATS

Abstract

Rainbow Smelt are the primary cold-water forage species in Lake Oahe, South Dakota, yet most aspects of their life history remain mysterious. In larval fish, growth and mortality are considered linked processes. Local reservoir habitat and resource availability have the potential to influence larval growth rates and affect mortality rates. As the larval phase is critical to eventual year class formation, we examined Rainbow Smelt larval emergence and growth patterns in the springs of 2017-2018. Larval surveys consisted of night trawls during spring 2017- 2018. We also mapped trawling sites using down-imaging commercial sonar, in addition to evaluating site temperature and zooplankton abundance. A subset of larva were measured and aged ($n = 249$). Rainbow Smelt emergence lasted longer in 2018 (56 days) than 2017 (28 days), although 2017 frequency distributions indicate sampling may have captured only partial trends. In 2018, growth differed by lake region and survey period. Notably, the regional instantaneous growth rates were higher in the southern region ($G = 0.017$) than the north region ($G = 0.009$). The southern zone displayed significantly slower warming and overall cooler water temperatures. We used a PCA to condense our physical habitat metrics. Temperature conditions were linked to the PC1 physical habitat gradient (77% of cumulative variance), with steep slope, deep, soft bottom sites warming more slowly than low slope, shallow, hard bottom sites. Zooplankton density was significantly lower at the southern sites, likely due to a combination of reservoir productivity gradients and

significantly higher larval Rainbow Smelt densities. Thus, we showed that the southern reservoir sites exhibited higher larval Rainbow Smelt densities that grew more quickly despite cooler conditions, potentially demonstrating a larval Rainbow Smelt thermal optima.

Introduction

The larval stage of fishes has long been acknowledged as critical for eventual recruitment (Hjordt 1926), and the preferred habitat during this period is often a combination of thermal and structural features (Houde 2008). These optima contribute to enhanced larval growth. In many northern fishes, higher growth in the first year of life leads to a larger body size going into a fish's first winter, increasing chances of survival (Michaletz 2010). Identification of preferred habitat for larva of a given species is therefore an important step to understanding recruitment in a system.

Rainbow Smelt *Osmerus mordax* spawning typically takes place soon after ice out across their range (Creaser 1925). The relationship between time to hatch and temperature appears to be nonlinear. Cold temperatures result in longer hatch times (2°C - 78 days | 4°C - 55 days) than warmer temperatures (8°C - 24 days | 10°C - 17 days, Owens 1982). Stream spawning produces larva that rear in stream estuaries and near-shore lacustrine habitats, before moving offshore into deeper, cooler habitat (O'Brien et al. 2012). Larva produced from main lake shoreline and reef spawning occur in similar areas to where they emerged, prior to moving into deep water (Tin and Jude 1983). Larval growth and survival is density-dependent and differs between habitats, based on temperature and zooplankton resources (O'Brien et al. 2012). Thus, different habitats likely contribute differentially to Rainbow Smelt recruitment in a system.

In Lake Oahe, South Dakota, Rainbow Smelt are the primary forage species for Walleye *Sander vitreus*, the dominant sport fish in the system. As Walleye condition is highly dependent on Rainbow Smelt abundance, factors relating to Rainbow Smelt

recruitment are important for managers. To further understand Rainbow Smelt recruitment to the larval phase, we examined 1) larval occurrence and emergence patterns, 2) spatial differences in larval growth across the reservoir, and 3) possible explanations for differences in growth including Rainbow Smelt density, zooplankton density, temperature, and habitat.

Methods

Study Area – Lake Oahe is the second largest reservoir on the Missouri River, stretching 372 km from central North Dakota to central South Dakota (Figure 5.1). At normal pool, Lake Oahe’s surface area measures 145,000 ha, with 3,623 km of shoreline with a multitude of embayments, and an overall shoreline development index of 27.4 (Nelson and Walburg 1977). The upper portion of Lake Oahe in South Dakota is mesotrophic, and transitions to oligotrophic downstream toward the dam (Fincel 2011). While Rainbow Smelt are constrained to the stratified southern 169 km (68,500 ha) of the reservoir during the summer (Burczynski et al. 1987), temperature conditions following ice-out allow adult Rainbow Smelt access to the entire reservoir for spawning.

Larval Sampling and Processing – Larval trawls were collected during the springs of 2017 and 2018. Each spring was divided into 3 periods, with 7-10 days between the periodic sampling visits, depending on weather. Trawling took place in two reservoir zones, north and south (Figure 5.1), with 5 sites per zone (Figure 5.1 insets). Zone and site locations were selected following hydroacoustic assessment of spawning Rainbow Smelt, outlined in Chapter 4. During each site visit, 3 replicate larval trawls were taken, yielding 15 trawls per zone per period. Trawling site order was randomized on each visit, with

sampling starting 30 minutes after sundown. Night sampling was necessary because larger Rainbow Smelt larva exhibit net avoidance during daylight hours (Tin and Jude 1983). Sites were selected to include the variety of habitat types present at each zone, based on visual assessment. Trawling was conducted with a 1 m diameter, 500 μ m mesh ichthyoplankton surface trawl, which was fitted with a flow meter to determine water volume and eventual catch density. Trawl samples were preserved in 95% ethanol (O'Brien et al. 2012, Bradbury et al. 2006, Ganger 1999). Rainbow Smelt preserved in 95% ethanol have been experimentally shown to only shrink 1.12%, with shrinkage not statistically different those fixed in formalin (Sirois et al. 1998). A single vertical zooplankton tow was taken from two times the Secchi depth at each site (Fincel 2011), using a 0.5 m diameter net with 300 μ m mesh, with Secchi depth approximated by readings taken in complete darkness beneath a 300 lumen headlamp. Zooplankton were preserved in 10% Lugol's solution. We subsampled 10% of the original sample volume in 2 ml increments. We identified and counted the zooplankton in each 2 ml subsample using a counting wheel under magnification. The density of zooplankton at a site (Z_D , #/L) was calculated using:

$$Z_D = \frac{Z_S * V_S * 1,000}{V_W}$$

where Z_S is the number of zooplankton in the 10% subsample, V_S is the volume (ml) of the subsample liquid, and V_W is the volume of the water column sampled during field work (Fincel 2011).

Rainbow Smelt larva were sorted and measured under magnification to standard length with dial calipers to $\pm 25 \mu$ m. For each site per period per year, if more than 20

Rainbow Smelt were caught, a random subsample of 20 larva were selected for aging (Simonin et al. 2016). If less than 20 individuals were sampled, all larva collected at a site were aged. Sagittal otoliths were removed using fine wire needles and mounted to a glass microscope slide using 80% balsam/20% xylene media. Otoliths were then photographed using imaging software under a compound microscope using transmitted light. Cross-polarization filters and image white balance were adjusted on an individual basis to obtain the best quality otolith images. As mounting larval otoliths proved difficult, we excluded from analysis any damaged otoliths, otoliths problematically oriented within or obscured by the mounting media, or otoliths from which we could not obtain a quality image. The remaining otoliths were consensus aged using three readers (Quist and Isermann 2017).

Larval Habitat and Mapping – We developed explanatory habitat metrics for larval Rainbow Smelt abundance and growth. We recorded visit-specific thermal conditions by calculating the mean of a 10 m temperature profile at trawling location, excluding the highly variable 1 m surface layer. To generate site-specific variables describing bathymetry and structural habitat attributes, we mapped the trawling locations in 2018 using a Lowrance HDS 7 unit with 200kHz HDI transducer. Three mapping transects were laid out parallel to shore using 2018 TerraColor Landsat 8 aerial imagery mosaics (Earthstar Geographics 2018). The outermost transect was at 50m, and the innermost was as reasonably close to the shoreline as could be accomplished without running aground. The middle transect was 25m from shore, with occasional deviations to cover bathymetric features of interest (e.g. prominent reef). Transects were mapped at 8

kmph, and slowed depending on wave interference and real-time visual assessment of sonar performance.

Post-processing was completed by BioBase (2018). Output was a 2D point cloud with depth, slope, and bottom hardness attributes, encompassing the shoreline at the trawling stations and extending 50 m offshore. The point cloud was subsequently rasterized, following recommendations from BioBase (2018) and used the Feature to Raster tool in ArcGIS 10.4 (ESRI 2016). From this, we calculated the vector ruggedness measure (VRM), which measures terrain ruggedness as the variation of 3D orientation in neighborhood cells, condensing slope and aspect variance into a single measure (Sappington et al. 2007). We applied this terrestrial metric as an index of bathymetric habitat complexity, and favored it over other options because it is less correlated to slope as other derived ruggedness metrics (Sappington et al. 2007). We used site mean values for habitat variables to simplify analyses.

We condensed the habitat variables (depth, slope, bottom hardness, and VRM) into a single descriptive metric using a principle components analysis (PCA) in R (R Core Team 2018) using the “stats” package (R Core Team 2019) to minimize collinearity concerns for further analyses. We checked the data for normality using normal QQ-plots, and assessed collinearity with Pearson’s correlation tests. Despite collinearity, we included mean depth, slope, bottom hardness, and VRM in the PCA, and examined the component loadings. We retained the first component as an independent variable describing a habitat type gradient.

Statistical Analysis – We iteratively fit a segmented breakpoint regression to larval Rainbow Smelt length at age (R library “segmented,” Muggeo 2008). The segmented breakpoint regression was used to capture two distinct periods growth in length (Simonin et al. 2016). We used the break-point regression equations to assign ages to the unaged larva. From this complete sample, both aged and estimated, we determined a distribution of larval emergence dates.

We examined larval Rainbow Smelt growth by fitting exponential growth curves to the daily mean length at age data:

$$a_{ei} = l^{(G*a_i)}$$

where a_{ei} is the estimated age at time i , l is the initial length or y-axis intercept, G is the instantaneous growth coefficient, and a_i is the observed daily mean length-at-age for the sample, following O’Brien et al. (2012). Models were fit using the R package “stats,” and an ANCOVA was used to determine if growth differed between survey periods in 2018; the 2017 larval catches were insufficient to be included in this analysis.

To further understand the differences in growth rates, we examined the potential for density-dependent and density-independent growth limitation. Peak larval density between sites in 2018 was compared with a single-factor ANOVA. We also compared mean zonal Daphnia density with a t-test. For density-independent factors, we used a 2-way ANOVA to compare mean temperature between the north and south zone by survey period. Following this, we used a correlation test to compare the habitat summary statistic to the grand mean temperature (mean of temperature profile means) for each site in 2018. As a final extension of these relationships, a multiple regression

was used to describe how temperature and habitat interacted to influence peak larval density across sites.

Results

We sampled more larval Rainbow Smelt in 2018 ($n = 295$) than in 2017 ($n = 56$, Figure 5.2). In 2017, the south zone ($n = 48$) had more individuals sampled than the north ($n = 8$). In 2018, the south zone ($n = 233$) again had more individuals sampled than the north ($n = 62$). Spring temperature was different between 2017 and 2018. In 2018, ice-out was three weeks later than 2017. This was coupled with quicker warming than 2017, yet within-year temperature between sites remained variable.

All habitat metrics were significantly correlated and collinear ($p < 0.05$). The first two components of the habitat PCA for the two zones dominated the loadings (Table 5.1). Depth and slope dominated the loadings, describing 100% of cumulative variation. We retained the first component scores as a summary statistic describing a habitat gradient, as this component represented 99% of the cumulative variance. Higher PC1 scores were associated with deeper, steeper sites, and generally a softer bottom. Lower PC1 scores correlated with shallow, low slope sites, with a harder bottom.

Using all the aged larva ($n = 241$), we estimated ages for the remaining subsample of fish ($n = 111$) using the iteratively fit breakpoint regression. The single breakpoint of the linear regression was 30.63 days (15.96 mm). The younger fish displayed faster growth (steeper slope, Figure 5.4). The estimated and observed ages were pooled to produce emergence schedules (Figure 5.5). Larval emergence patterns in the north zone cannot be accurately defined for 2017, because few individuals were

detected on all dates. In the south zone, the highest frequency of emergence was around Julian day 123 (May 3). In the north zone in 2018, two small emergence peaks were observed on days 113 (April 23) and 128 (May 8). In the south zone in 2018, the highest emergence was recorded day 135 (May 15). Although the distribution seemed to be centered on that date, there were potentially several more pulses. Generally, emergence of larval Rainbow Smelt lasted approximately 40 days.

We divided the 2018 data by survey period and zone (Figure 5.6), and the subsequent ANCOVA comparing the growth curves was significant. In the north zone (Table 5.3), we assumed the higher initial length values (y-intercept) reflected the lack of sampled larva ≤ 10 mm, along with the lower zonal slopes (G). The south zone had a more complete range of larval sizes represented, leading to lower I values. The south zone growth rates were higher between survey periods (Table 5.3), leading to longer site-specific mean lengths-at-age (Figure 5.7).

The ANOVA of peak mean density by site was significant ($F = 18.33$, $df = 9$, $p < 0.0001$). The Tukey's HSD post-hoc tests showed 3 of the 5 southern sites had higher larval densities than the remaining sites (Figure 5.6). A paired t-test of mean *Daphnia* spp. density was significant ($t = -4.45$, $df = 14$, $p = 0.0003$), with lower *Daphnia* density in the south zone (2.65 ± 1.65 , mean \pm 95% CI) compared to the north zone (10.06 ± 3.05).

For density-independent variables, the 2-way ANOVA of temperature by survey period and zone was significant (Table 5.3). The south zone was cooler than the north zone early in the season. It eventually warmed to similar temperatures by the third period (Figure 5.8). The cooler southern sites were also deeper and steeper than the

northern sites (Figure 5.9). The northern sites were shallower (Figure 5.9) and consistently warmer (Figures 5.8, 5.9). A multiple regression of the habitat – temperature interaction was significant (Figure 5.10, p -value = 0.0457, $adj. r^2 = 0.57$), and the highest larval densities were predicted at the deep, steep, cooler temperature sites. The lowest densities were predicted on the shallow, low slope, and higher temperature vector. Few Rainbow Smelt are expected at sites with a mean depth < 2.14 m and a slope declination < 7°, based on the regression and back-transformation of PC1 scores.

Discussion

Higher larval densities were observed in the south zone of Lake Oahe in both years, yet 2017 densities were far lower across sampling sites. This may be linked to the different spring temperature patterns. Site bathymetry had a pronounced influence on water temperature, likely through warming rates, although this was not experimentally evaluated. Somewhat counterintuitively, the cooler and higher density southern zone displayed faster growth rates. Additionally, zooplankton densities in the lower zone were also lower compared to the upper zone.

While the 2017 warming duration was generally driven by regional weather patterns, the differential site warming observed in 2018 was likely the result of bathymetry. As light absorption and diminution of light energy via transformation to heat is curvilinear with increasing depth (Wetzel 2001), it naturally follows that shallower sites typically warm quicker than deeper sites, as we observed. Warmer waters generally result in faster hatching times for Rainbow Smelt (O’Brien et al. 2012)

in a nonlinear pattern (Owens 1982). This conceivably leads to a longer first growing season, which is important as growth and mortality are linked processes during larval fish development (Houde 1987). Increased growth generally equates to increased survival and subsequent contribution to overall year class strength. In our observations, emergence dates for the warmer north zone were earlier (Figure 5.5), yet these larval fish grew slower in 2018 (Figure 5.6).

Larval fish growth can be influenced by a variety of factors, among which are adequate forage (Hjort 1926, Cushing 1990) and temperature (O'Brien et al. 2012). Zooplankton densities at spawning sites were represented by *Daphnia* spp., which are a preferred food item for adult Rainbow Smelt in Lake Oahe (Karnitz 1992). *Daphnia* densities were lower in the southern zone, where the larval densities were highest. As adult Rainbow Smelt locally depress zooplankton size structure and density (Karnitz 1992), the lower southern zone density may partially be the result of larval fish foraging. The southern zone is also generally less productive (Fincel 2011), which also could lead to lower zooplankton density. The actual cause of the zooplankton abundance trend remains unclear.

Concurrent with the larval density pattern, mean temperature within the southern zone ranged from 9.1 – 18.8°C, with the north zone 16.5 – 20.0°C. The slower southern warming (Figure 5.8) lead to sampling duration mean temperatures of approximately 14°C. The preferred temperature of young-of-the-year Rainbow Smelt is 13 – 14°C (Brandt et al. 1980), and temperatures in this range have resulted in larval growth rates exceeding growth rates at sites with temperatures above or below that

range (O'Brien et al. 2012). Generally, 6 – 13°C is an optimal range selected by Rainbow Smelt (Becker 1983), with the highest densities occurring 10 – 16°C (Tin and Jude 1983). Our multiple regression analysis of habitat, temperature, and larval density predicted the highest concentrations at temperatures below 14°C. Thus, it appears the faster larval Rainbow Smelt growth in the southern zone resulted from preferred thermal habitat, despite the high population density.

The high Rainbow Smelt larval density was associated with habitat that lead to a thermal optimum. To exploit the linkage between growth and survival previously described, Rainbow Smelt larva exhibit vertical swimming behaviors to maintain position in optimal habitats in estuarine habitats (Bradbury et al. 2006). These behaviors typically begin at 10 mm (Bradbury et al. 2003), after the larva have floated downstream from spawning locations (Bradbury et al. 2006). As most of the larval Rainbow Smelt we examined were ≥ 9 mm (Figure 5.4), they may have been maintaining position in an optimal nearshore habitat, similar to lotic populations. Alternatively, this behavior may have biased the catches of our surface trawl if larva were avoiding wind-driven surface currents. This is impossible to evaluate *ex post facto*; however, a variety of gears has been used to successfully sample larval Rainbow Smelt across habitat types, including a modified purse seine (Ganger 1999), a 30 cm stationary drift net (Bradbury et al. 2006), various midwater trawl designs (Simonin et al. 2016, O'Brien et al. 2012, Brown 1995, Tin and Jude 1983), bottom trawls (Brown 1995) and surface trawls (O'Brien et al. 2012, Tin and Jude 1983).

Offshore transport may have diminished densities of larval Rainbow Smelt in the northern zone, giving the appearance of a higher density southern population. In Lake Superior, higher May rainfall was correlated with poor Rainbow Smelt recruitment, with the increased rainfall potentially washing larva into the pelagic zone of the lake (Hoff 2004). In that environment, neither thermal nor zooplankton conditions were optimal. The north zone of Lake Oahe's fetch is exposed on a northwest – southeast compass bearing (Figure 5.1). As the predominant spring wind directions fall along this bearing, larva in shoreline habitats would be exposed to wind-driven currents and wave action. The southern zone fetch is perpendicular to the predominate spring wind direction, limiting wind-driven influences. Newly hatched Rainbow Smelt larva (5 – 9 mm) are found in surface aggregations, likely due to positive buoyancy (Bradbury et al. 2006), and larvae < 10 mm exhibit limited swimming ability and show no ability to maintain position in surface or bottom layers (Fortier and Legget 1982). Thus, newly emerged Rainbow Smelt larva may have been carried offshore in the northern zone, and subsequently were not vulnerable to our sampling.

Management Implications

While managers can do little to manage larval fish, beyond ensuring proper rearing habitat is available, understanding recruitment to the larval phase is nonetheless a useful tool. This understanding allows prediction, in a general sense, of potential larval production, which is foundational for year class strength. For Lake Oahe's Rainbow Smelt, it appears that 3 weeks of warming, post-ice-out, to 13 – 15°C is associated with higher larval densities. In theory, if this occurs earlier in the year and both temperatures

and zooplankton abundances are favorable, a longer growing season should lead to greater length-at-age at first overwintering, increasing survival on this all-important first step to strong year class formation.

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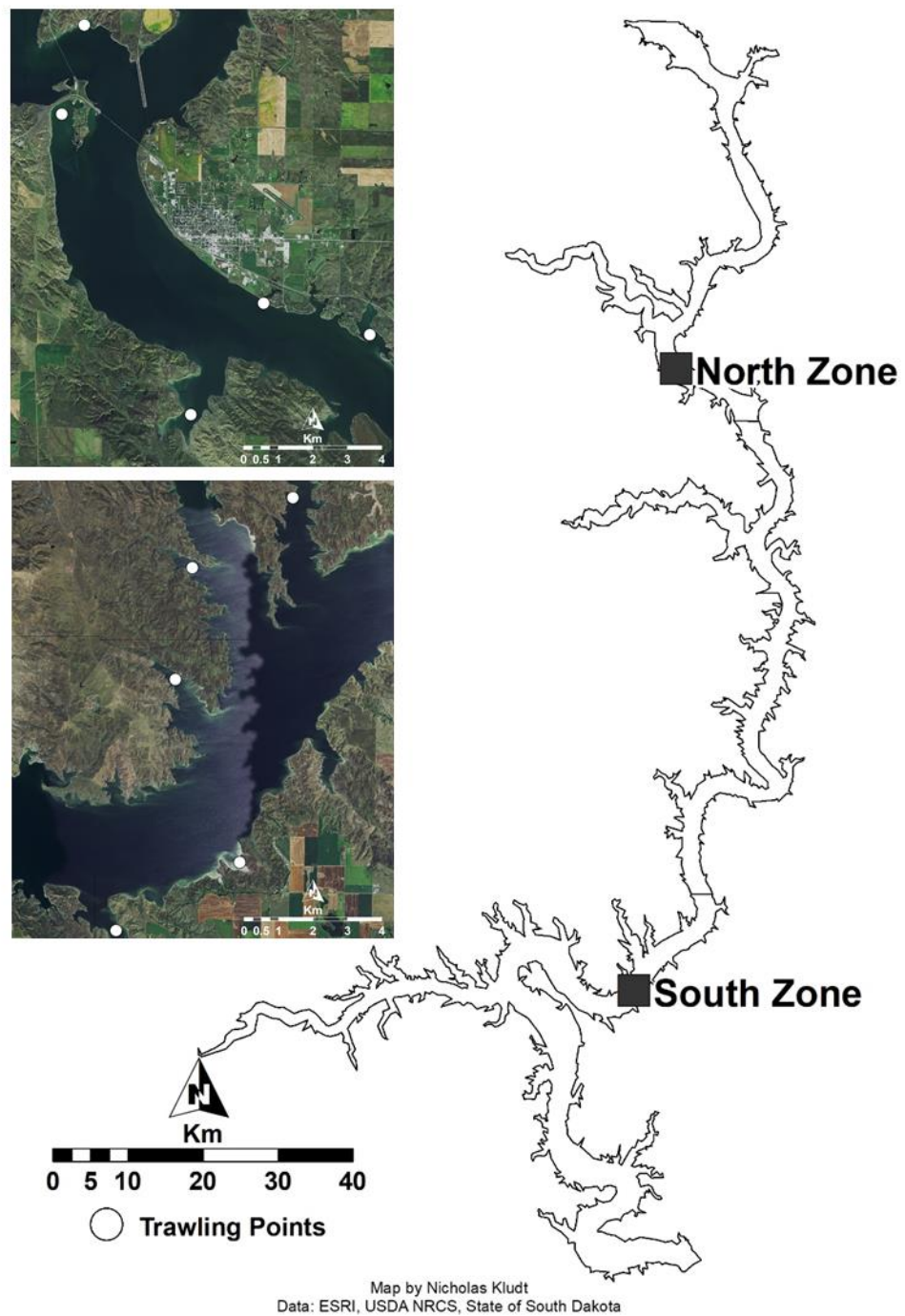


Figure 5.1: Rainbow Smelt larval trawling regions, Lake Oahe, South Dakota. North (top inset) and south (bottom inset) trawling zone detail, with site locations.

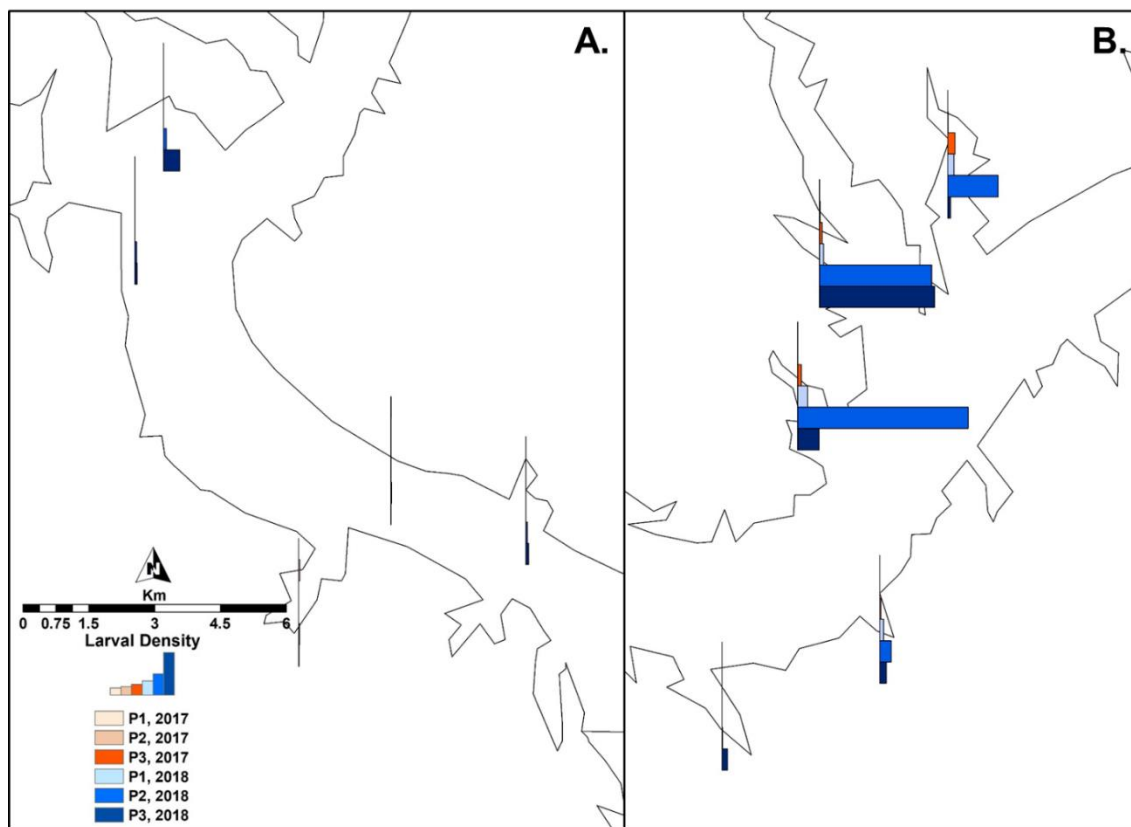


Figure 5.2: Relative comparison of larval Rainbow Smelt mean density ($\#/m^3$) by survey year, period, and site for north (A.) and south (B.) trawling zones. Mean density determined from 3 replicate larval tows per site, P1 = survey period 1, P2 = survey period 2, P3 = survey period 3.

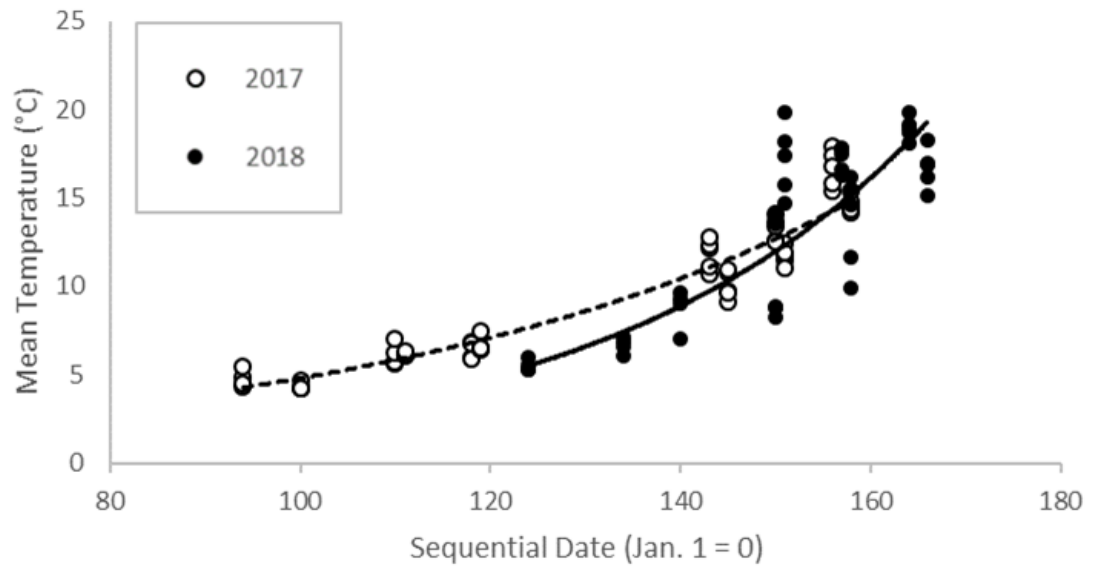


Figure 5.3: Spring warming rates, 2017 and 2018, as determined from temperature profiles taken during larval trawling and earlier spawning adult surveys.

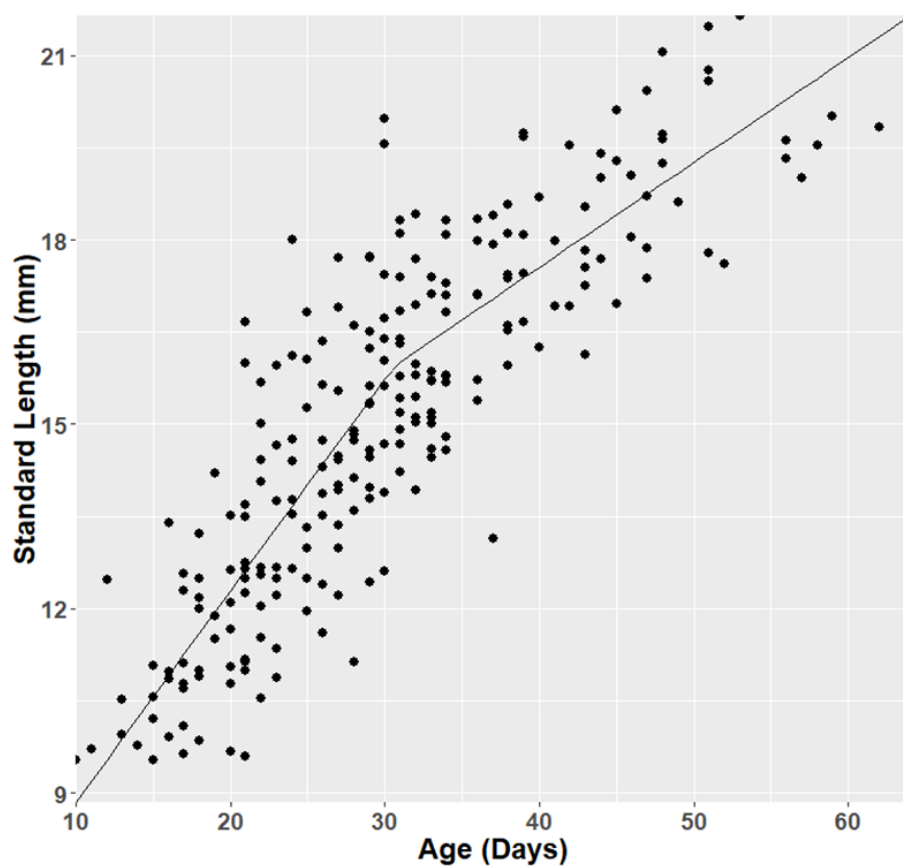


Figure 5.4: Pooled break-point regression of Rainbow Smelt length-at-age. The single breakpoint in pooled length-at-age was 30.63 days, 15.96 mm. Linear equations: lower segment $y = 0.3447x + 5.3979$, upper segment $y = 0.1706x + 10.7310$.

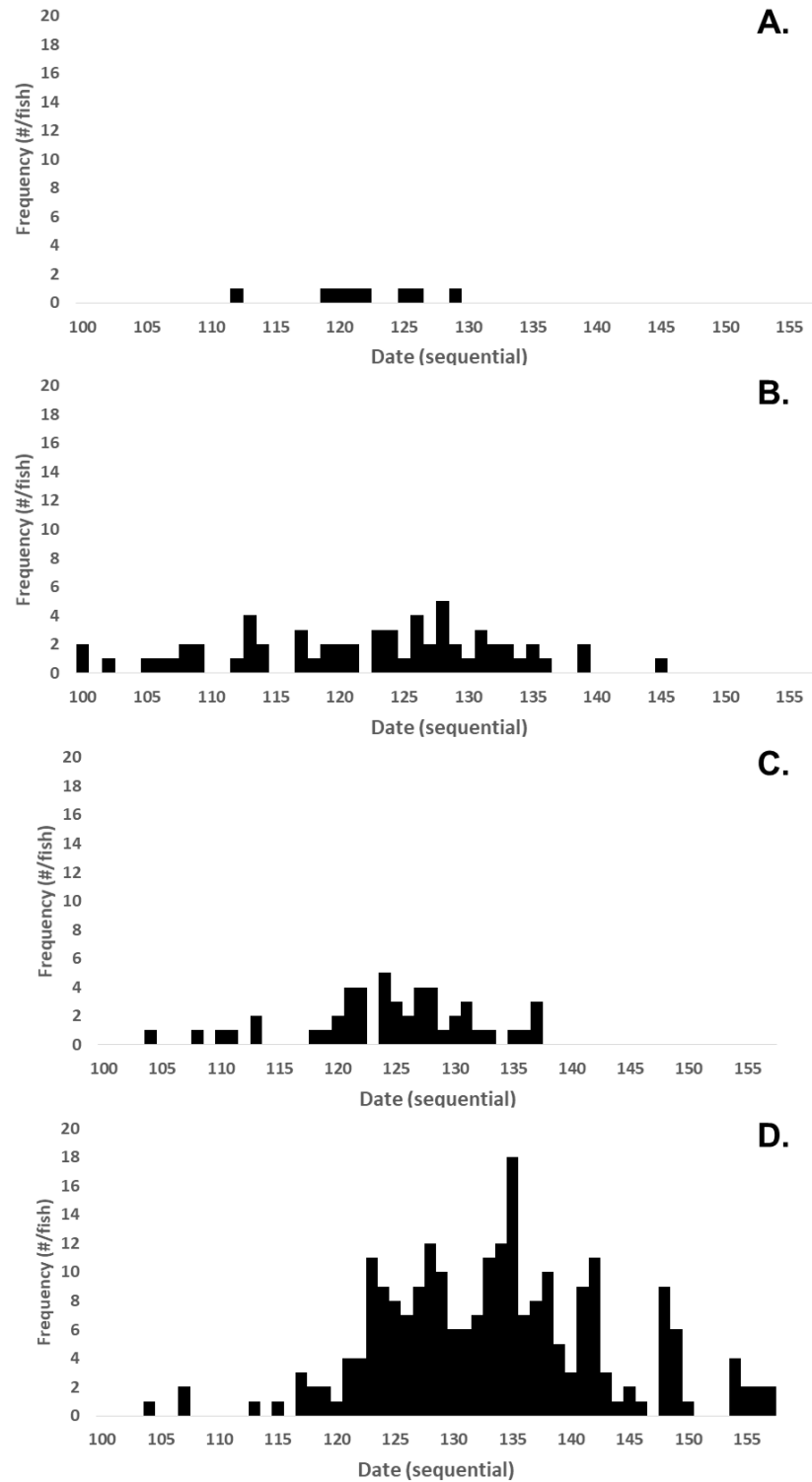


Figure 5.5: Emergence distributions Rainbow Smelt by date, north zone 2017 (A.), 2018 (B.), south zone 2017 (C.), 2018 (D.).

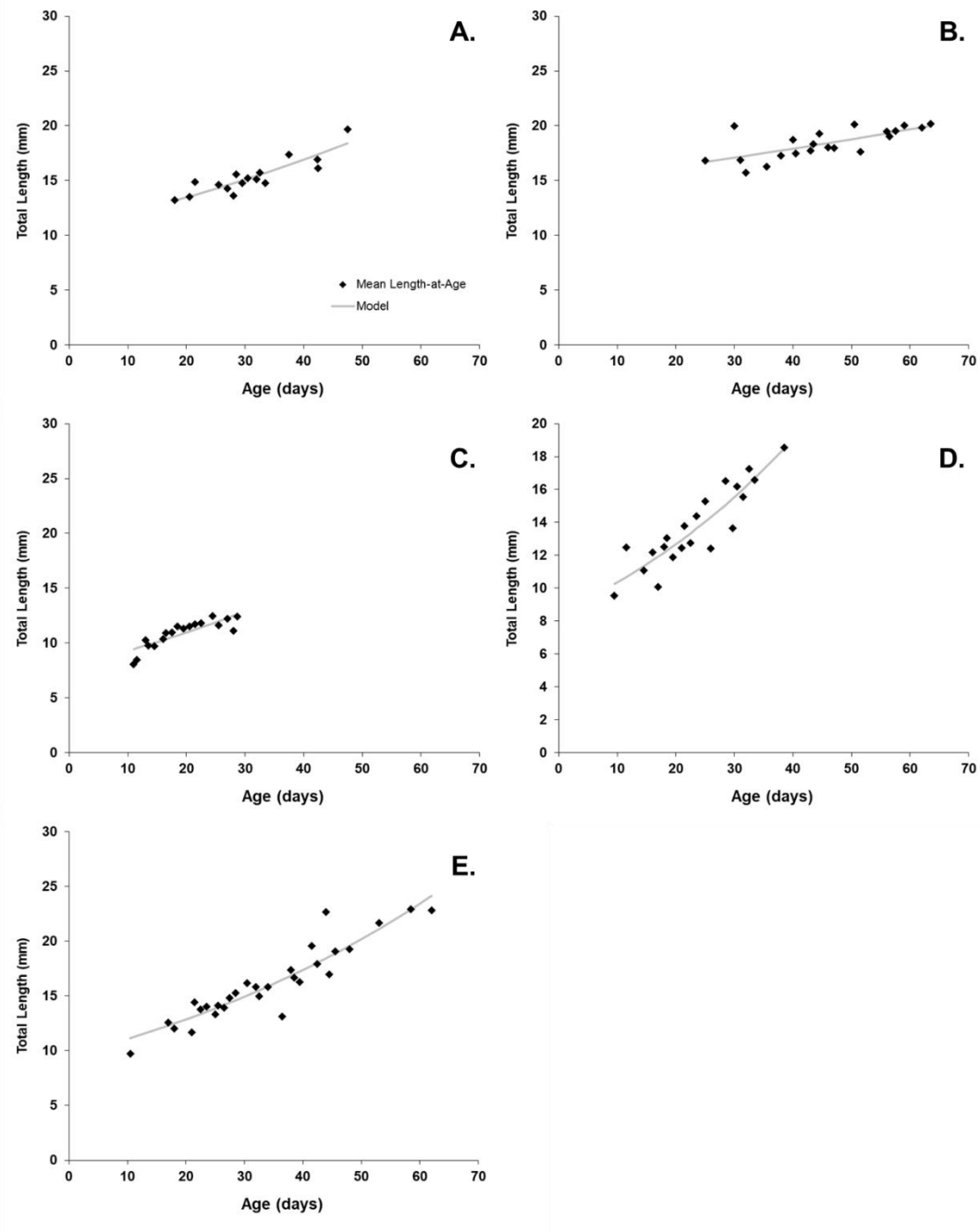


Figure 5.6: Exponential larval Rainbow Smelt growth curves for 2018, north zone period 2 (A.), 3 (B.), south zone period 1 (C.), 2 (D.), and 3 (E.). No larva were sampled in period 1 in the north zone. Regression coefficients are reported in Table 5.2.

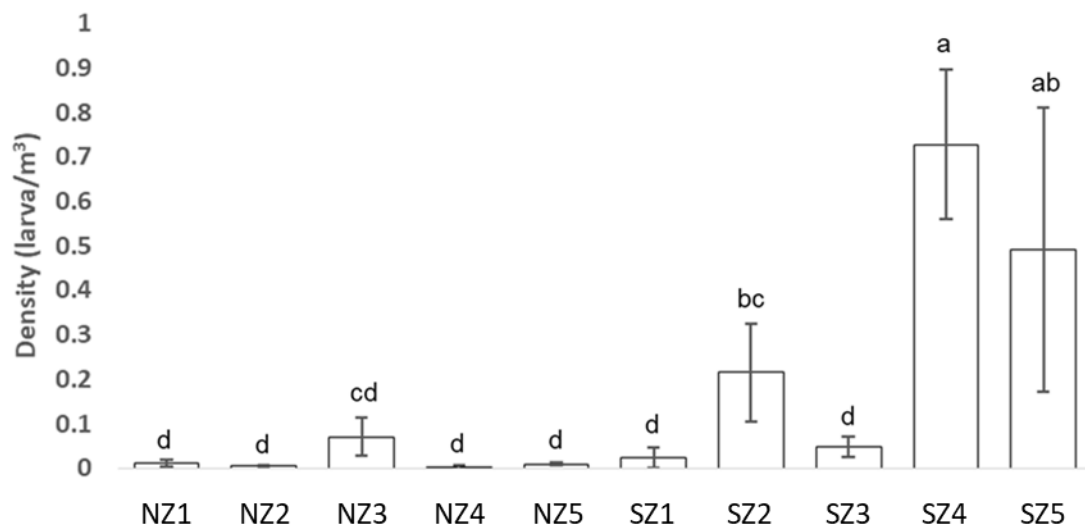


Figure 5.7: Rainbow Smelt 2018 peak mean larval density by site (\pm 95% confidence interval), illustrating the general trend of greater abundance in the south zone. Site location xZy, where x = north or south zone, and y = site number. Letters represent groupings from Tukey's HSD post-hoc, following significant single-factor ANOVA ($F = 18.33$, $df = 9$, $p < 0.0001$).

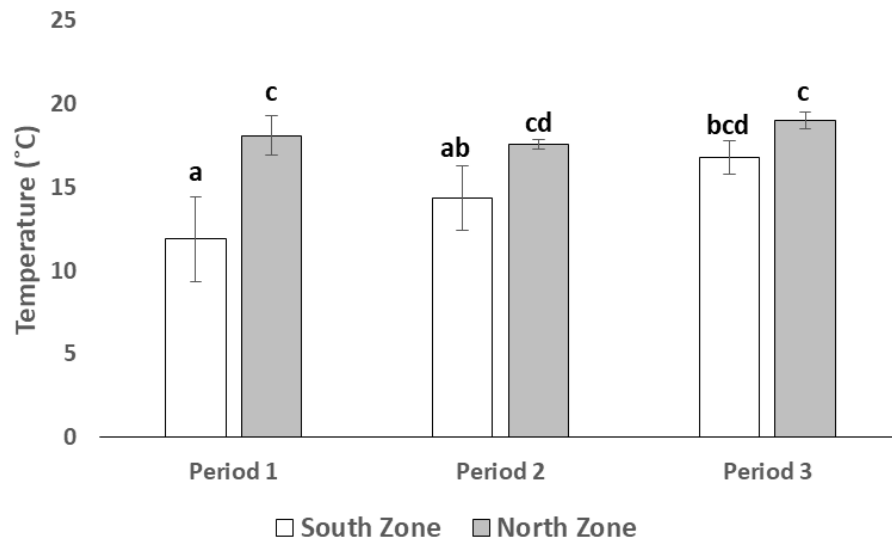


Figure 5.8: Mean 2018 temperature by survey period and zone (\pm 95% confidence interval). Letters represent groupings from Tukey's HSD post-hoc, following significant 2-way ANOVA (Table 5.3).

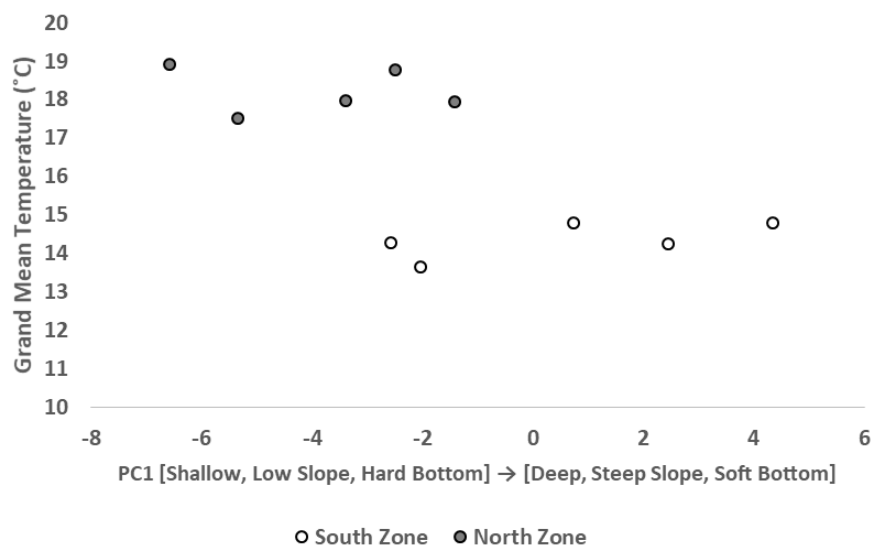


Figure 5.9: Site habitat summary statistics (PC1) and 2018 temperature grand means (mean of temperature profile means) by trawling zone, 2018. Pearson's $r = 0.79$.

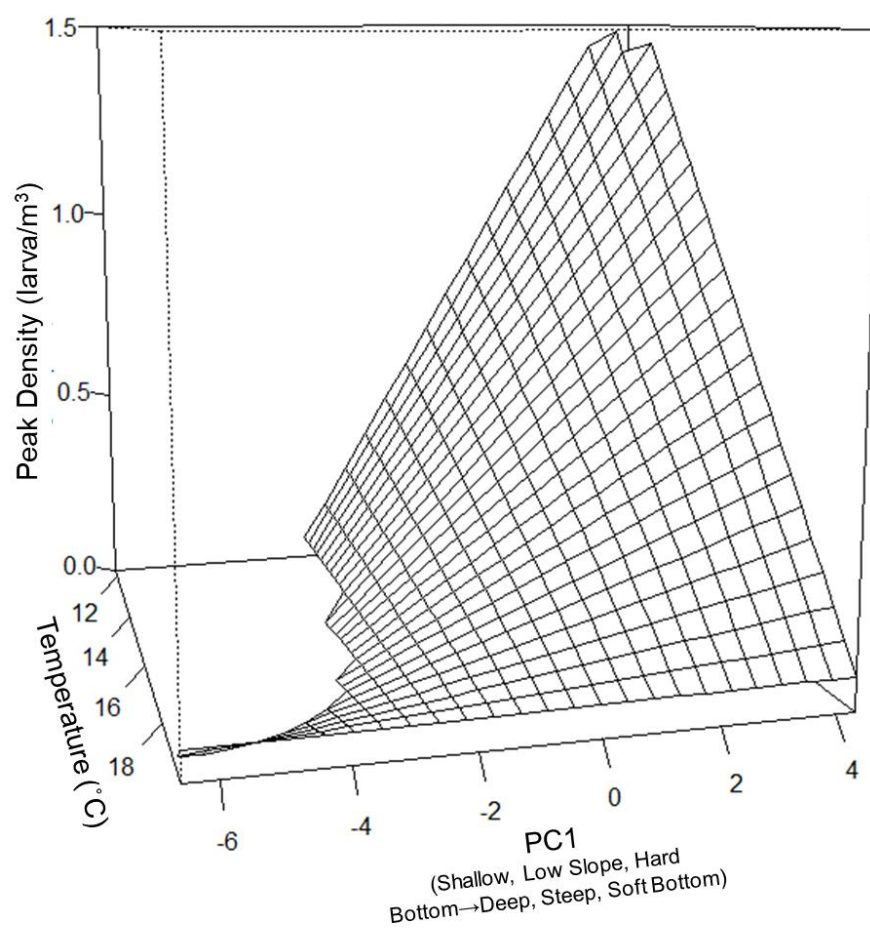


Figure 5.10: Multiple regression of 2018 peak larval Rainbow Smelt detections by habitat (PC1) and temperature (°C, F -value = 4.97, p -value = 0.0457, $adj. r^2 = 0.57$)

Table 5.1: Principle components analysis results of physical habitat variables. PC1 values, retained for analysis, represent a gradient, with higher values indicating a steeper, deeper, softer bottomed site.

	Comp. 1	Comp. 2
Standard Deviation	3.468	0.267
Cumulative % Variance	0.994	1.000
Loadings:		
Mean VRM	-	-
Mean Depth	-0.539	0.842
Mean Slope	0.842	0.539
Mean Hardness	-	-

Table 5.2: Exponential larval Rainbow Smelt regression coefficients for 2018 by survey period. No larva were captured in period 1, north zone. l = initial length or y-axis intercept, G = instantaneous growth coefficient, r^2 = coefficient of determination.

	Period	l	G	r^2
North Zone	2	10.7432	0.0113	0.78
	3	14.8368	0.0047	0.49
South Zone	1	7.8701	0.0165	0.71
	2	8.4443	0.0203	0.81
	3	9.5238	0.0150	0.86

Table 5.3: 2-way ANOVA of mean temperature by survey period and trawling zone, 2018.

	df	F - value	p -value
Period	2	7.85	0.0023
Zone	1	40.223	<0.0001
Period:Zone	2	3.796	0.0369

CHAPTER 6: A CASE HISTORY OF RAINBOW SMELT AS A RESERVOIR FORAGE FISH IN
LAKE OAHE, SOUTH DAKOTA

Abstract

Fisheries management often is focused on providing desirable sizes and abundances of sport fish to anglers. As sport fish growth depends in part on available prey, forage fish management is an integral part of the management process, and has a well-established history in the United States. Managing forage species, however, can be challenging. To maximize production, they need to exhibit high recruitment, high mortality from predation (ensuring they are effective at supporting predator growth), and high growth that ensures overwinter survival but doesn't limit availability to sport fish. Rainbow Smelt *Osmerus mordax* and Cisco *Coregonus artedii* are important prey for Walleye *Sander vitreus* in Lake Oahe, South Dakota, and they exemplify some of these forage fish management challenges. Using long-term monitoring data, we investigated Rainbow Smelt and Cisco recruitment at the reservoir scale. Rainbow Smelt recruitment was driven by heating degree days (a proxy for spring temperature) and reservoir elevation. Cisco recruitment, which previously occurred only at low levels, was released by Rainbow Smelt population collapses. Walleye body condition in Lake Oahe has been closely linked to Rainbow Smelt availability for decades. Recently, Walleye condition has not correlated with Rainbow Smelt abundance, likely the result of recent Cisco recruitment and high Gizzard Shad *Dorosoma cepedianum* production. In Lake Oahe, Rainbow Smelt will continue to be impacted by entrainment, as high spring flows severely reduce the population. In these events, it is expected that Cisco will be released

from Rainbow Smelt predation and competition and produce strong year classes. While a short lag may occur, Cisco and Gizzard Shad ought to provide alternative prey for the Lake Oahe Walleye population while also providing a predation buffer to enable Rainbow Smelt population recovery.

Introduction

Predicting recruitment is one of the most challenging aspects of fisheries management (Hilborn and Walters 1992). The relationship between stock size and recruitment has historically relied on time series correlations between density-dependent (e.g. intra- and interspecific) and density independent (e.g. environmental) factors (Ricker 1975). Although density dependent inter-and intraspecific predation is important, environmental conditions and annual variance thereof often match or exceed the influence of changing stock size (Ricker 1975). Variables such as temperature, precipitation, discharge, and reservoir elevation are common density-independent recruitment drivers for reservoir fishes (Allen et al. 2009). Although managers are sometimes able to control reservoir elevation and discharge, this is complicated in large reservoirs with competing water use priorities (Allen et al. 2009).

Forage fish management has been a cornerstone of inland fisheries management in the United States for over 70 years. Early work established the practice of managing piscivorous sport fish growth and mortality based on forage abundances (Swingle 1951). Early reservoir forage management included trial-and-error stocking approaches, with associated unpredictability (Magnuson 1976). As forage management matured, principles were established regarding effective practices. Ney (1981) outlined six principles still widely used by managers for selecting forage species for reservoirs. A forage fish is considered suitable if it is reproductively prolific, generally stable in population abundance, trophically efficient, vulnerable to predation, non-emigrating, and innocuous (Ney 1981). A forage fish ought to consistently exhibit high recruitment,

high mortality from predation, and growth that doesn't inhibit availability to sport fish. Of these, assessing and managing recruitment can be the most difficult.

Rainbow Smelt *Osmerus mordax* in Lake Oahe, South Dakota, are a case study that exemplifies some of these challenges. Lake Oahe is a major main-stem reservoir on the Missouri River managed jointly by North Dakota Game and Fish Department (NDGF) and South Dakota Department of Game, Fish and Parks (SDGFP). Rainbow Smelt were first detected in Lake Oahe in 1972, following a 1971 stocking by NDGF in Lake Sakakawea, 165 km upstream of Lake Oahe. The species became established in Lake Oahe by the late 1970s and was the impetus for creating a 2-tiered fishery. Soon, Rainbow Smelt became the primary forage species for Walleye *Sander vitreus*, with Walleye condition highly correlated to Rainbow Smelt relative abundance through time (Felts 2018, Graeb et al. 2008). Direct angler use of Rainbow Smelt is rare, but a short-term spring recreational dip net and seine fishery exists at public access locations on the eastern shore of Lake Oahe during periods of high Rainbow Smelt abundance, excluding the lower reaches of the reservoir (Robert Hanten, Jr., SDGFP, personal communication).

In this study, we described the continuing temporal trends between Walleye and Rainbow Smelt. We also explored Rainbow Smelt recruitment, and their potential interactions with Cisco *Coregonus artedii*, the other major cold-water pelagic prey species in Lake Oahe. Our goals were to 1) describe the influence of Rainbow Smelt and the evolving prey base on the Walleye population in Lake Oahe, 2) characterize drivers of Rainbow Smelt and Cisco recruitment, and 3) provide a general discussion on the suitability of Rainbow Smelt as a reservoir forage species.

Methods

Study Site - Lake Oahe is the second largest storage reservoir on the Missouri River, stretching 372 km from central North Dakota to central South Dakota (Figure 6.1). At normal pool, Lake Oahe's surface area measures 145,000 ha, with 3,623 km of shoreline. Three major tributary arms, along with myriad embayments, provide complex littoral habitats, with an overall shoreline development index of 27.4 (Nelson and Walburg 1977). The upper portion of Lake Oahe in South Dakota is mesotrophic, sometimes approaching eutrophic, and transitions to oligotrophic downstream toward the dam, with nutrients and zooplankton decreasing appreciably (Fincel 2011). The lower 169 km of Lake Oahe, approximately 68,500 ha, annually stratify during the summer months (Burczynski et al. 1987), and support the 2-tier fishery. Rainbow Smelt spatial distribution is constrained by thermal habitat during this period.

Although Lake Oahe sport fishery is focused primarily on Walleye, the reservoir also supports populations of Smallmouth Bass *Micropterus dolomieu*, Sauger *Sander canadensis*, Channel Catfish *Ictalurus punctatus*, as well as low abundances of Northern Pike *Esox lucius*, Crappie spp. *Pomoxis spp.*, and White Bass *Morone chrysops*. Chinook Salmon *Oncorhynchus tshawytscha* have been stocked annually since the late 1980s. Cisco *Coregonus artedii* were introduced in the early 1990's to supplement the cold-water prey base. Other common prey fish species include Gizzard Shad *Dorosoma cepedianum*, Yellow Perch *Perca flavescens*, Spottail Shiner *Notropis hudsonius*, Emerald Shiner *Notropis atherinoides*, and various age-0 sport fish (Fincel 2011, Fincel et al. 2016b).

Fisheries Long-Term Monitoring – We used South Dakota Game, Fish and Parks (SDGFP) standard monitoring data to construct a 35-year time series of Walleye relative weight (W_r , Murphy et al. 1991), along with Rainbow Smelt and Cisco abundances. SDGFP monitoring techniques for the cold-water species have evolved with changing technology. Subsequently, we utilize two surveys to capture Rainbow Smelt population trends. Additionally, we utilize catch curve residuals and deep-water gill net catches to index the Cisco population. We reasoned that an effect magnitude would be large if separate modeling of the same species and the same covariates revealed similar relationships, despite the gear differences between times series.

The Lake Oahe standard cool water adult sportfish population survey, from which we obtained our Walleye condition time series, was conducted each August, 1985-2016. At each of the standard survey locations ($n = 9$), three gillnets were deployed in a straight line between anchors, pulled taut, and set overnight (approximately 20 h) and on the bottom within depth zones of 0–10 m and 10–20 m for a total of six nets per site. Nets were randomly set parallel and transverse to bottom contour lines. If part or all of a gillnet was unfishable due to wind or wave action, the partial catch was disregarded to not influence estimates of catch rates, and the gillnet was reset as soon as possible. The multifilament nylon gillnets were 91 m x 2 m with a 0.5 hanging ratio and 15 m panels of sequentially increasing bar mesh sizes: 13, 19, 25, 32, 38, and 51 mm (Finzel et al. 2019). In 2017 and after the AFS standard experimental gillnets were adopted (Bonar et al. 2019), which caused a slight change in net design. Additionally, nets were set in random locations and perpendicular to the shore. As we

concentrated on Walleye condition (W_r) instead of relative abundance (CPUE), we did not use any correction factors to account for this change in sampling methods and gear.

The first Rainbow Smelt time series, 1985-2000, was a standardized cold-water gill net survey conducted annually in August. At the 3 standard sampling locations, 15 of the previously described multifilament gillnets were suspended at 27.5 m and set overnight (approximately 20 hours, Johnson et al. 1995)). From 1993-2000, an additional 15 m panel of 10 mm bar mesh was added to the nets for the cold-water survey, with the goal of increasing catch rates (Lott et al. 2001). We excluded the catch from the additional panel, as catch rates from both methods were highly correlated (Pearson's $r = 0.91$) and displayed similar CPUE trends.

The second Rainbow Smelt time series, 2000-2018, was the SDGFP hydroacoustic survey, conducted annually in July. As hydroacoustic methods and techniques have evolved, SDGFP monitoring protocols have also evolved. Thus, the hydroacoustic time series includes estimates derived from 3 separate methods.

The first hydroacoustic survey time period, 2000-2007, used a vertical beaming 200 kHz split beam HTI model 243 system (Hydroacoustic Technology Incorporated, Seattle), with 5 pings/s and 0.4 ms pulse duration. Rainbow Smelt density estimates used echo-integration, based on 2 m depth strata and a 120 s sampling sequence, amplified with a $20\log(R)$ TVG function (Nelson-Statsny 2001). It was assumed all fish ≥ 80 mm within or below the metalimnion were adult Rainbow Smelt (see Chapters 2 and 3), with length determination based on the Love (1977) target strength – length (TS) equation:

$$TS = 19.4 * \log_{10}(TL) - 0.9 * \log_{10}(f) - 62$$

where TS is the target strength of an individual fish, TL is the total length (cm) of the fish, and f is the frequency of the sonar pulse in kilohertz. Regression equations, predicting surface area (ha) from reservoir elevation (ft msl), were used to compute volume (m^3) for each 2 m strata in an area (Stone and Nealson 1990). In this era, abundance estimates were derived by multiplying mean regional hydroacoustic density by predicted reservoir cold water habitat volume. The transect locations were access driven ($n = 11$, Figure 6.1). Data from this era were accepted at face value, as we were not able to re-analyze the raw data.

The second hydroacoustic survey time period, 2008-2014, utilized the same transects ($n = 11$) as the prior era with different equipment and analysis methods. Hydroacoustic surveys were conducted using a Biosonics DT-X system with a vertical beaming 420 kHz split beam transducer with a 6.9° circular beam angle. Survey settings were 5 pings/s with a 0.5 ms pulse duration. System calibration was periodically checked according to the manufacturer's instructions using a 17.5 mm tungsten carbide target sphere and the apparatus described by Foote et al. (1987). We re-analyzed the raw data collected during this period using the single echo detection biomass option with 40-log(R) time varied gain within Sonar5-Pro (Balk et al. 2015) for consistency with the current analysis methodology. We excluded a 0.5 m layer immediately above the lake bed to eliminate bottom interference (Parker Stetter et al. 2006, Simmonds and MacLennan 2005). To convert 1 dB TS intervals to approximate fish length and assign a species identification to that density interval (#/ha per 1 db), we used the TS equation

from Love (1977). Based on length-frequency distributions generated from deep-water gillnetting targeting areas of high acoustic target density, we designated fish 100 – 179 mm as age 1+ Rainbow Smelt. We then used a spatial interpolation technique for data expansion, using transect centroids as our input location for transect density. Inverse distance weighted (IDW) interpolation was used to interpolate densities. The IDW formula is expressed:

$$\hat{Z} = \sum_{i=1}^n \frac{1}{(d_i)^p} Z_i \bigg/ \sum_{i=1}^n \frac{1}{(d_i)^p}$$

where \hat{Z} is the estimated value for the prediction point, Z_i is the measured value of the sample point, d_i is the Euclidean distance between the sample point and prediction point, n represents the number of sample points and p is a power parameter (Li et al. 2018). The method is considered deterministic because the influence of a sample point on a prediction location is influenced by intervening distance, as opposed to a model-based approach. The method is recommended for evenly spaced systematic sampling (Li et al. 2018), and was conducted in R (R Core Team 2018) using the gstat package with the default smoothing factor $p = 2$ (Pebesma 2004). A distance threshold was applied (11.3 km), limiting the between-transect interpolation to the values of either up- or down-stream bounding transect.

The third hydroacoustic survey time period, 2015-2018, utilized the same equipment, settings, and analysis techniques outlined, the only change being a new systematic transect layout. The current survey format was adopted for even spatial coverage, as opposed to the access-driven historic survey layout. Under the historic

survey layout, some reservoir reaches were over- and under-represented (Figure 6.1). While feasibility of a systematic survey was limited historically by equipment and lake access points, recent equipment upgrades have made large-scale night surveys feasible and safer. While evolving hydroacoustic methods preclude statistically rigorous examination of this time series, we have corrected it to the best of our ability, and use it to describe the general trends associated with Rainbow Smelt populations throughout the 2000-2018 era.

Cisco were not abundant prior to the 2011 Missouri River flood, and were not indexed as part of the hydroacoustic survey prior to that year. Our abundance data is therefore limited. To describe recent recruitment trends, we used weighted catch curve residuals (Maceina 1997). Cisco were sampled during the SDGFP suspended gillnets that accompanied the hydroacoustic survey in July 2015. Suspended gill nets were 38.1 x 7.3 m, with 7.6 m multifilament nylon panels of bar mesh sizes in the following order: 19, 10, 13, 16, 25 mm. Cisco were randomly subsampled, and agreement of the sample ($n = 2655$) to subsample ($n = 75$) length-frequency distribution within 10 mm length bins was verified using a two-sample Kolmogorov–Smirnov test ($KS, \alpha = 0.05$). Cisco were consensus aged by three readers using thin-sectioned sagittal otoliths (Quist and Isermann 2017). This yielded a time series from 2002-2013. Additionally, we analyzed a second time series, Cisco catches from cold-water suspended gillnet survey from 1992 – 2000, which is the post-introduction period until the survey was discontinued. Gillnets and methods were consistent with those previously described for the historic Rainbow Smelt dataset.

Environmental Covariates – We used a suite of environmental covariates as predictors for Rainbow Smelt recruitment. As the majority of Rainbow Smelt detected in Lake Oahe are consistently age-3 fish (Lott et al. 2001, Kludt unpublished data), we applied a 3-year covariate lag to the CPUE estimate from either netting or hydroacoustics. Cisco catch curve residuals years were compared directly to annual estimates.

As water temperature data were not available spanning the temporal and spatial scale of this investigation, we used a regional April-May spring air temperature average from 3 NOAA weather stations. The stations (Pierre, Gettysburg, and Mobridge, South Dakota) spanned the latitudinal gradient of Lake Oahe, and are representative of the reservoir-wide air temperature trends for a given spring. We used the same approach for heating degree days, from the same NOAA stations. Heating degree days for a given spring period are the sum of the differences between daily mean temperature and 18.3°C. A higher spring heating degree day value indicates a cooler spring period.

We used several methods to describe spring flow and precipitation. From the same NOAA weather stations as above, we calculated the mean total April-May precipitation. We thought this metric would described the influence of the many small creeks and streams flowing into Lake Oahe’s embayments, long thought to be important habitat for Rainbow Smelt spawning. We also used the annual maximum monthly outflow, as this captures the major flooding Lake Oahe periodically experiences, which results in mass entrainment of adult Rainbow Smelt biomass and attendant population crashes (Fincel et al. 2016b). We also included mean annual reservoir elevation to

capture the wet-dry cycles of the South Dakota prairie. We thought this may be important due to large recruitment pulses of other species when the reservoir refilled after prolonged drought cycles, leading to a trophic upsurge (Pegg et al. 2015).

Statistical Methods – We used an information theoretic multiple regression approach to evaluate the influence of the environmental covariates on Rainbow Smelt abundances. Two separate analyses were run. The first used the hydroacoustic estimates as the dependent, referred to as the “contemporary” analysis, and the second used the cold-water suspended gillnet CPUE, referred to as the “historic” analysis. Normality and tolerance values were assessed for both time series and associated independent variables. In both the contemporary and historic datasets, mean reservoir elevation and monthly outflow were \log_{10} transformed. Rainbow Smelt gillnet CPUE was likewise transformed. All other variables were normally distributed. Models were ranked by ΔAICc , with a $\Delta\text{AICc} \geq 4$ threshold was used to differentiate candidate model performances from the intercept (null) model performance (Burnham and Anderson 1998). We judged the relative importance of independent variables by assessing the AICc weights (W_{AIC}) of all candidate models that included that variable (MacKenzie et al. 2006). While interaction models were explored, none improved upon the single-factor models presented. Analysis was conducted in R using the library “AICcmodavg” (Mazerolle 2019).

We used the same approach for the Cisco weighted catch curve residuals, analyzed using the “FSA” R library (Ogle 2019). We included the estimated Rainbow Smelt abundance as an independent variable for the “contemporary” Cisco analysis;

likewise, in the “historic” Cisco analysis, we included the Rainbow Smelt cold-water gillnet CPUE. Other independent variables were as described above, along with modelling and interpretation. Instead of a time lag, we directly compared the Cisco dependents to the catch curve residuals and the cold-water CPUE. For the latter, we chose this approach because Cisco had just been introduced to the reservoir, and it is likely they were not yet naturally reproducing.

Results

The long-term Walleye W_r was z-standardized around the mean (86.27 ± 4.88 , mean \pm SD) to show the variance through time in response to prey base fluctuations (Figure 6.2). In the historic period, 1985 – 2000, Lake Oahe Walleye experienced the first of several negative periods of W_r depression. The first major Rainbow Smelt crash followed the boom Rainbow Smelt CPUEs of 1993-1994. The negative trend was compounded by high flows in 1997 associated with the Missouri River flooding, and subsequent Rainbow Smelt entrainment. Cisco, introduced in the early 1990’s began appearing in the survey as the population expanded through the mid-1990’s, with CPUE increasing after the Rainbow Smelt crash. Unfortunately, the survey was discontinued in 2000, so the trend is limited and incomplete. Rainbow Smelt stocks began recovering throughout the modern period, 2000 – 2018, as assessed by the annual hydroacoustic surveys (Figure 6.2). Despite the potential errors associated with the evolution of Lake Oahe hydroacoustic survey methods, the abundance trend was confirmed as Walleye W_r recovered concurrently. During this period, Gizzard Shad abundance also increased in the reservoir, as assessed by the warm-water shoreline seining survey, although that

trend was not sustained (Figure 6.3). In 2009, Walleye condition peaked, concurrent with the production of the largest Walleye year class on record (Felts 2018). The following two years saw a slight decline in W_r , followed by a major decline in 2012. This followed the 2011 flood, which again led to major Rainbow Smelt entrainment (Fincel et al. 2016b) and was responsible for the 2011-2012 crash of the then-recovering Rainbow Smelt population (Figure 6.2). Following the 2011 Rainbow Smelt crash, Cisco stocks expanded to the highest abundances observed since their introduction. Concurrent with the Cisco increase, mean Walleye W_r increased to record levels in 2018 (Figure 6.2). This increase was concurrent with a Gizzard Shad CPUE peak (Figure 6.3). Thus, it appears that although Rainbow Smelt and Walleye W_r remain closely linked, the availability of alternative forage species may be decoupling this relationship.

The Rainbow Smelt recruitment modelling used the same suite of independent variables for the historic and contemporary datasets. The historic time series showed 95% of W_{AIC} was associated with mean annual reservoir elevation (Table 6.1). Higher Rainbow Smelt CPUE was associated with lower mean annual reservoir elevations (Figure 6.4). No other models were investigated due to the high weight associated with reservoir elevation.

The contemporary time series showed heating degree days was an important influence on recruitment, with 62% W_{AIC} (Table 6.2). The null, or intercept, model was also strongly supported at 24% W_{AIC} . This model, along with reservoir elevation ($W_{AIC} = 10\%$, $\text{adj. } r^2 = 0.09$), were separated by $< 4.00 \Delta AICc$ from the top model. The top model's fit was also relatively poor ($\text{adj. } r^2 = 0.27$). Greater estimated Rainbow Smelt

abundance was associated with lower spring heating degree days (Figure 6.5), indicating a preference for an earlier, warmer spring. Model fit could be improved by the exclusion of the 2010 datapoint ($\text{adj. } r^2 = 0.43$). In 2010, reservoir elevations peaked as Lake Oahe completed refilling after a drought period (Figure 6.6), and the large relative abundance of Rainbow Smelt observed that year may have resulted from recruitment during the refilling period.

Cisco recruitment modelling used the same covariates, with the addition of Rainbow Smelt CPUE (historic) and abundance estimates (contemporary), depending on temporal range. The KS test of the 2015 Cisco subsample – overall sample length-frequencies suggested similar distributions ($D = 0.31$, $p = 0.0878$). The contemporary recruitment time series was based on subsample catch curve residuals (Figure 6.7, $\text{adj. } r^2 = 0.48$). Using the residuals as the response variable, the top model was Rainbow Smelt abundance (Table 6.3, 53% W_{AIC}), with the null model similar ($\Delta\text{AIC} = 1.54$) yet less supported (24% W_{AIC}). As all other models had less weight than the null and exceeded $\Delta\text{AIC} = 4$ from the top model, we only retained the Rainbow Smelt model. Relatively larger Cisco year classes were not produced at higher Rainbow Smelt abundances (Figure 6.8), although the fit of this regression was relatively poor ($\text{adj. } r^2 = 0.29$). In the immediate post-introduction period from 1992-2000, the null model was the top model and most models were similar to it ($\Delta\text{AIC} < 4$). Generally, models performed poorly (Table 6.4). Nonetheless, elevated Rainbow Smelt CPUEs were associated with lower Cisco CPUEs (Figure 6.9, 26% W_{AIC} , $\text{adj. } r^2 = 0.31$). While this relationship is a direct comparison of CPUE, as opposed to the lagged abiotic factors, we find it interesting the

newly introduced Cisco CPUE increased markedly after 1997, a flood year. This trend is similar to the 2013-14 Cisco year class production (Figure 6.7) and subsequent abundance increase (Figure 6.2), which followed the 2011 flood and entrainment-related Rainbow Smelt collapse.

Discussion

Lake Oahe Walleye condition has long been responsive to Rainbow Smelt abundance (Felts 2018, Graeb et al. 2008, Davis 2004); thus, Rainbow Smelt recruitment has a direct impact on the sport fishery. That recruitment is driven by a combination of spring weather and reservoir elevation. Alternative cold-water prey abundance via Cisco recruitment is largely driven by depressed Rainbow Smelt abundance. While we were not able to rigorously evaluate the mechanisms of that interaction, it has been explored in other systems (e.g. Myers et al. 2009). Gizzard Shad are stocked by SDGFP in periods of depressed cold-water prey (Fincel et al. 2017). The Gizzard Shad supplemental stocking strategy and warm-water habitat preference likely render them independent from cold-water prey dynamics. Nevertheless, the abundance of these alternative prey species in recent years may be decoupling the long-established linkages between Rainbow Smelt relative abundance and Walleye condition.

In the historical data range (1985-2000), lower reservoir elevations coincided with higher recruitment of Rainbow Smelt, as assessed by the cold-water suspended gill net survey. Lower water surface elevations generally result in differential habitat availability (Pegg et al. 2015), which can influence Rainbow Smelt recruitment dynamics (Feiner et al. 2015). In Lake Oahe, lower surface elevations result in dewatering of

shallow embayment habitat, which may increase the relative proportion of the shoreline that is composed of deeper and steeper bathymetry, as the shoreline contracts to the edge of the pre-reservoir Missouri River bluffs. This bathymetry has been identified as important for spawning (Chapter 3) and larval rearing (Chapter 4) in Lake Oahe.

Conversely, increasing reservoir elevation was found to improve Walleye recruitment in Lake Oahe (Felts 2018), likely as part of the trophic upsurge and increased rearing habitat availability associated with inundation of terrestrial habitats as a reservoir refills after a period of lower water levels (Pegg et al. 2015, Miranda et al. 1984). The two largest Rainbow Smelt CPUE pulses in this period were 1993 and 1994, coincidental with a reservoir-refilling period (Figure 6.6). Rainbow Smelt age composition percentiles in 1993 (age-2 = 56.6%, age-3 = 37.3%) and 1994 (age-2 = 48.6%, age-3 = 42.8%, Lott et al. 2001) indicated production occurred at the lower reservoir elevation prior to refilling. These two sampling years also were the only instances of age-2 Rainbow Smelt being more numerous than age-3 detections.

In the contemporary data range (2000-2018), lower heating degree days coincided with higher recruitment of Rainbow Smelt, as assessed by the hydroacoustic surveys. Practically, this indicates warmer spring weather increases Rainbow Smelt recruitment. We interpreted this in two ways.

First, as growth and mortality are linked processes during larval fish development (Houde 1987), spring thermal conditions optimal for faster larval growth result in greater larval survival (O'Brien et al. 2012). Chapter 4 highlighted the thermal differences between two habitat types, with cooler water and gradual warming

producing faster growth and greater larval density than rapidly warmed environs. Lower heating degree day values are evidence of this process, as higher values can be attributed to longer winters followed eventually by rapid warming. Conversely, Rainbow Smelt are eurythermal, with thermal tolerance dependent on life stage (Parker-Stetter et al. 2006). As epilimnetic water temperature increases, larval Rainbow Smelt mortality rates decline as adult Rainbow Smelt move into deeper, cooler water (Simonin et al. 2016). As cannibalism is a major feature limiting Rainbow Smelt recruitment (Rooney and Paterson 2009, Gorman 2007, Hoff 2004, Henderson and Nepszy 1989), thermal separation of larva and adults may be important for year class formation.

Second, a lower heating degree day total can indicate an earlier spring, which contributes to a longer growing season. A longer growing season conceptually leads to larger body size for first overwintering, which generally increases survival, leading to greater recruitment. Greater size increasing over-winter survival has been observed in age-0 Coho Salmon *Oncorhynchus kisutch* (Quinn and Peterson 1996), Bluegill *Lepomis macrochirus* (Shoup and Wahl 2011), Largemouth Bass *Micropterus salmoides* (Fullerton et al. 2011), Walleye (Grote et al. 2018), Cisco (Pangle et al. 2011), and Sand Smelt *Atherina boyeri* (Henderson et al. 2006). We expect these processes to interactively benefit Rainbow Smelt recruitment in Lake Oahe.

Some uncertainty remains regarding Rainbow Smelt recruitment in Lake Oahe. Although we speculate that favorable habitat for Rainbow Smelt recruitment increased at lower reservoir surface water elevations from 1985-2000, the elevation variable may act as a proxy for an as-yet unidentified causal factor. We also concluded the “reservoir

reset” (Felts 2018) resulting from the 1993-1994 refilling period was not responsible for the increased Rainbow Smelt recruitment in the same period, yet showed a large year class was likely produced concurrent with the 2007-2009 refilling. While reservoir elevation and temperature are fairly common density-independent factors affecting fish recruitment, one or more unknown variables seemingly remain to be clarified.

The only variable explaining Cisco recruitment in the historic and contemporary data ranges was the relative abundance of Rainbow Smelt. This is not surprising, as Cisco can be either suppressed or extirpated by Rainbow Smelt in small lake systems (Hrabik et al. 1998, Evan and Loftus 1987). Conversely, restoration of small lake Walleye populations has increased predation pressure on Rainbow Smelt, indirectly leading to Cisco recovery (Krueger and Hrabik 2005). While small lake dynamics are documented, relationships become more equivocal in larger systems (Myers et al. 2009). On a regional scale in Lake Superior, Cisco recruitment to age-1 and Rainbow Smelt biomass were negatively correlated, while site-scale Cisco recruitment was more influenced by abiotic factors (Rook et al. 2013). Cisco recruitment can be repressed through predation pressure on larva (Hoff 2004, Myer et al. 2009) and/or competition for zooplankton resources (Rooney and Paterson 2009). In Lake Superior, estimated larval Cisco mortality from Rainbow Smelt predation ranged from 15 - 100% (Myers et al. 2009). Rainbow Smelt can outcompete native zooplanktivores (Scott and Crossman 1973), and their ability to restructure zooplankton community size structure has been documented in Lake Oahe (Karnitz 1992). Thus, while abiotic variables may influence Lake Oahe Cisco recruitment on a site or reach scale, Rainbow Smelt are likely impacting recruitment on

a reservoir scale. The noise in the statistical relationships is likely the result of localized abiotic factors. Thus, it appears the Lake Oahe cold-water prey base exhibits desirable dynamics. When Rainbow Smelt collapse, Cisco recruitment is released until Rainbow Smelt stocks recover and re-exert pressure.

Walleye growth rates are often influenced by prey abundance and community composition. Fast growth is often observed when vulnerable, energetically rich pelagic species are available, such as Rainbow Smelt (Fincel et al. 2014, Jones et al. 1994) or Cisco (Kaufmann et al. 2009). Conversely, Walleye populations that are known to prey heavily on Rainbow Smelt typically see declines in condition when the Rainbow Smelt population declines or crashes. Systems where this pattern was observed include Horsetooth Reservoir (755 ha; Johnson and Goettl 1999), Lake Oahe (450,00 ha; Graeb et al. 2008, Fincel et al. 2016a, Felts 2018), and Lake Winnipeg (2,451,00 ha; Geoff Klein, Manitoba Conservation and Water Stewardship, unpublished data). Given the extreme scale differences, we suggest that Walleye condition is likely to be responsive to Rainbow Smelt fluctuations in systems where the two coexist.

In Lake Oahe, though, this dynamic appears to have recently weakened. Walleye condition (W_r) has recovered without a corresponding increase in Rainbow Smelt abundance, potentially caused by recent increases in Gizzard Shad and Cisco abundances. A Gizzard Shad introduction resulted in increased Walleye growth rates in a western South Dakota reservoir (Ward et al. 2007), and Gizzard Shad use in Lake Oahe has continued into the present. In Lake Oahe, adults have been supplementally stocked as an emergency Walleye prey subsidy during Rainbow Smelt crashes (Fincel et al.

2017). In the absence of Rainbow Smelt, Gizzard Shad are consumed heavily, but availability of age-0's is limited to late summer (< 3 months) thus limiting their ability to meet Walleye annual energy requirements (Fincel et al. 2014). In Fort Peck Reservoir, Montana (99,150 ha), Cisco dominate Walleye diets (Mullins 1991), and an analysis of 215 Ontario lakes showed Walleye females achieved a larger asymptotic length in lakes where Cisco were available (Kaufman et al. 2009). A study of Walleye muscle enzymes showed Walleye were less active when Cisco were present (Kaufman et al. 2006), and more empty Walleye stomachs occurred in Cisco lakes in the Ontario study (Kaufman et al. 2009). Together, the two previous examples suggested that the availability of large, calorically rich Cisco decrease Walleye activity and increase growth. Given that Gizzard Shad and Cisco abundances have recently increased in Lake Oahe with marginal Rainbow Smelt recovery, it is conceivable that the sole reliance of Walleye on a single forage species has weakened under present circumstances.

Rainbow Smelt as a forage species present both opportunities and challenges. They are highly adaptable, assuming adequate thermal conditions are available, and are found in estuarine systems, a variety of small inland lakes, the Great Lakes, large Missouri River reservoirs, and western reservoirs (Creaser 1925, Rupp 1959, Mullins 1991, Johnson and Goettl 1999, Scott and Crossman 1973, Graeb et al. 2008, O'Malley et al. 2017). Adults remain vulnerable to piscivores due to generally small size (Carlander 1969) and have a high energy density (Fincel et al. 2014). Reliance on a spring spawning run limits reproductive output relative to other species with multiple spawning bouts, such as Gizzard Shad. Rainbow Smelt recruitment is notoriously

eruptive and is characterized by boom-to-bust cycles (Gorman 2007, O'Brien 2014).

Thus, while Rainbow Smelt dominate diets where present, their highly variable recruitment limits their utility as a forage species. Additionally, some have suggested negative interactions with Walleye recruitment (Johnson and Goettl 1999), although this was not observed in Lake Oahe (Felts 2018). It would be unwise to further introduce Rainbow Smelt as a forage species due to the lack of recruitment stability, low relative production, and the potential for antagonistic effects on sport fish recruitment.

Management Implications

For management of Lake Oahe, Rainbow Smelt will continue to be impacted by entrainment, as high spring flows severely reduced the population on multiple occasions. It is expected that Cisco will be released from predation and/or competition by Rainbow Smelt declines and produce strong year classes following a Rainbow Smelt population crash. Although a short lag may occur, Cisco and Gizzard Shad ought to provide alternative prey for the Lake Oahe Walleye population during Rainbow Smelt recovery. In Lake Superior, high Cisco biomass provided a buffer from predation which allowed Rainbow Smelt stocks to recover (Gorman 2007). It is possible this may occur in Lake Oahe, and we would expect that Rainbow Smelt would eventually repress the Cisco population once sufficient biomass is achieved. Gizzard Shad emergency stocking of select embayments is an effective tool for subsidizing Walleye in the absence of cold-water prey, and ought to be employed following Fincel et al. (2017).

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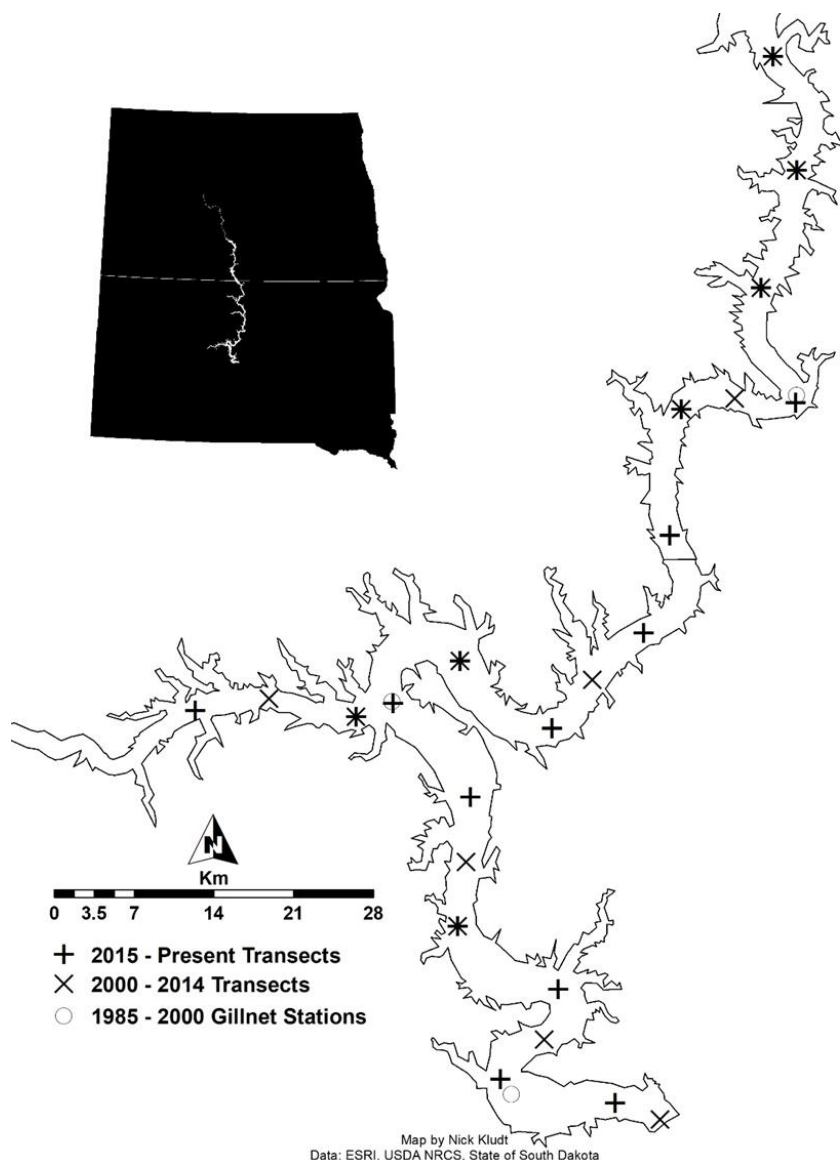


Figure 6.1: Lake Oahe standard monitoring locations, 1985 – present, for hydroacoustic surveys and the historic cold-water netting survey. Transect 2015 – present refers to 0.7 km hydroacoustic transects centered over the historic thalweg of the Missouri channel, while 2000-2014 transects were cross sections of the reservoir. At each gillnet station, 15 experimental mesh gillnets were suspended at 27.5 m overnight. Inset shows Lake Oahe, relative to North and South Dakota.

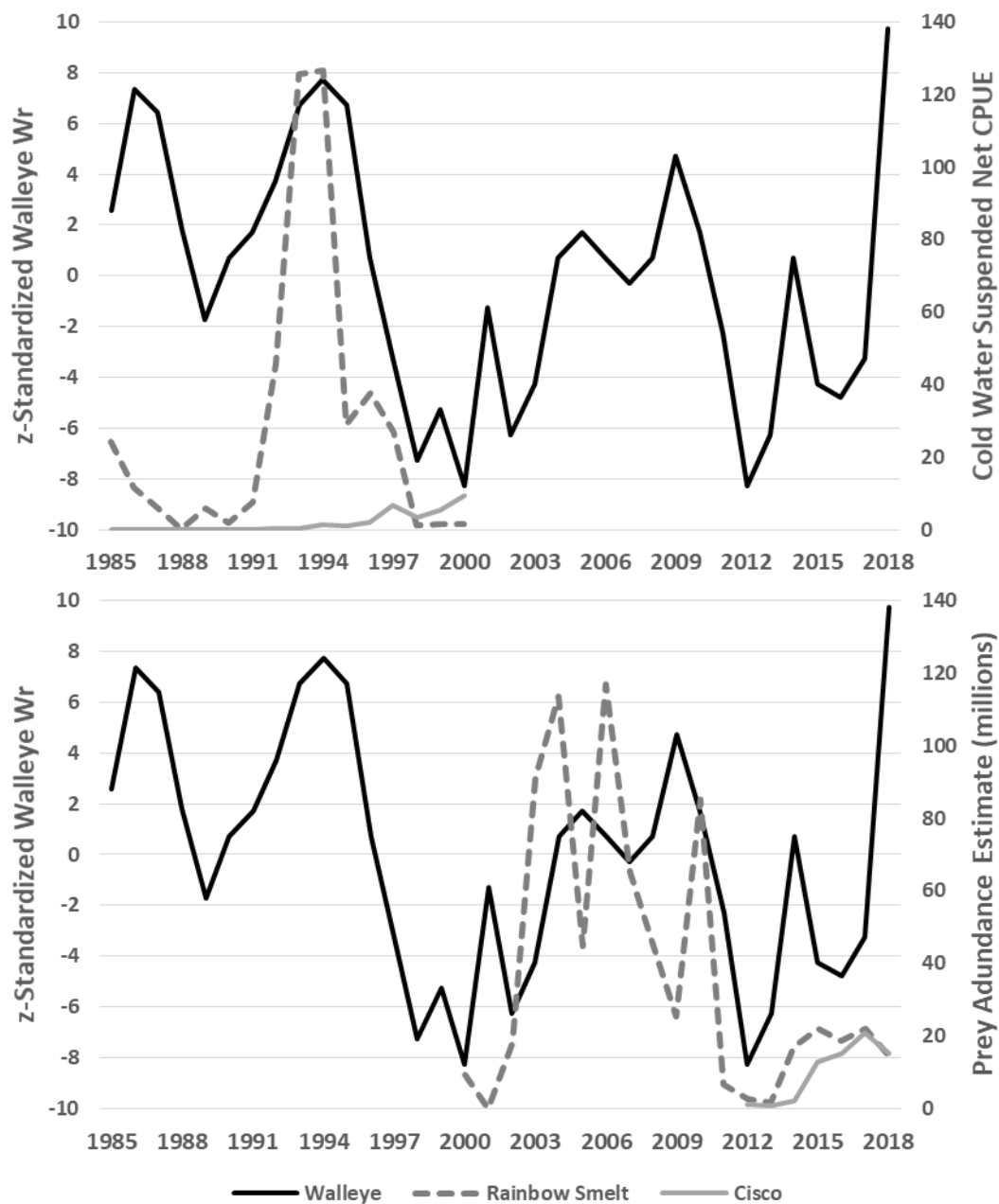


Figure 6.2: Lake Oahe Walleye z-standardized relative weight, 1985-2018, relative to historic cold-water suspended gill net CPUE of Rainbow Smelt and Cisco, 1985 – 2000 (top), and hydroacoustic abundance estimates of the same, 2000 – 2018 (bottom).

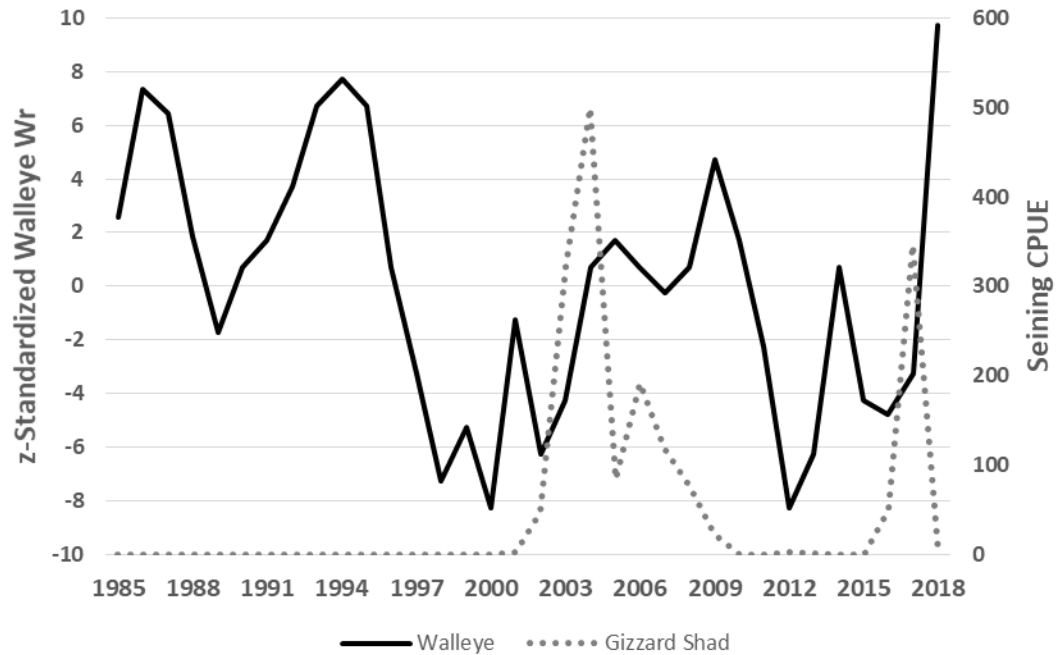


Figure 6.3: Lake Oahe Walleye z-standardized relative weight, 1985-2018, relative to seine survey Gizzard Shad CPUE estimates.

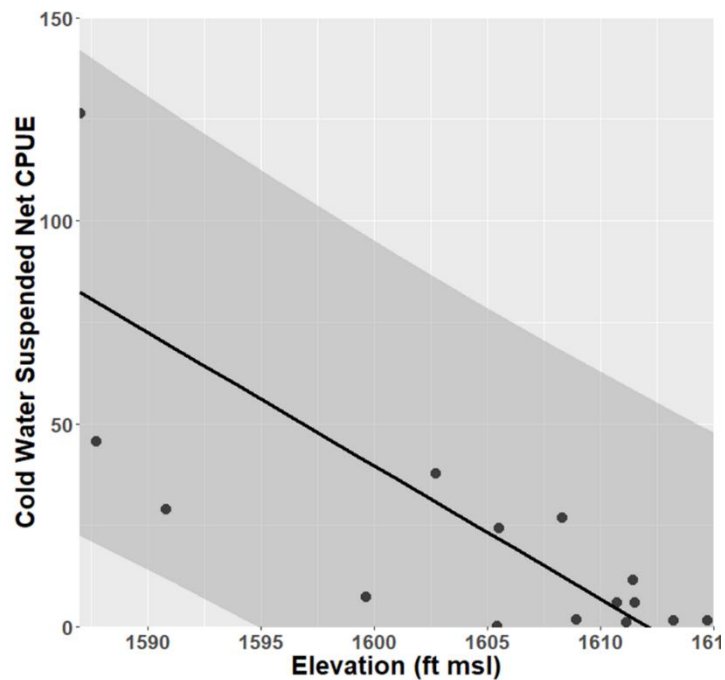


Figure 6.4: Rainbow Smelt cold-water suspended gillnet CPUE and annual mean reservoir elevation, $\text{adj. } r^2 = 0.62$. Shaded area represents 95% CI.

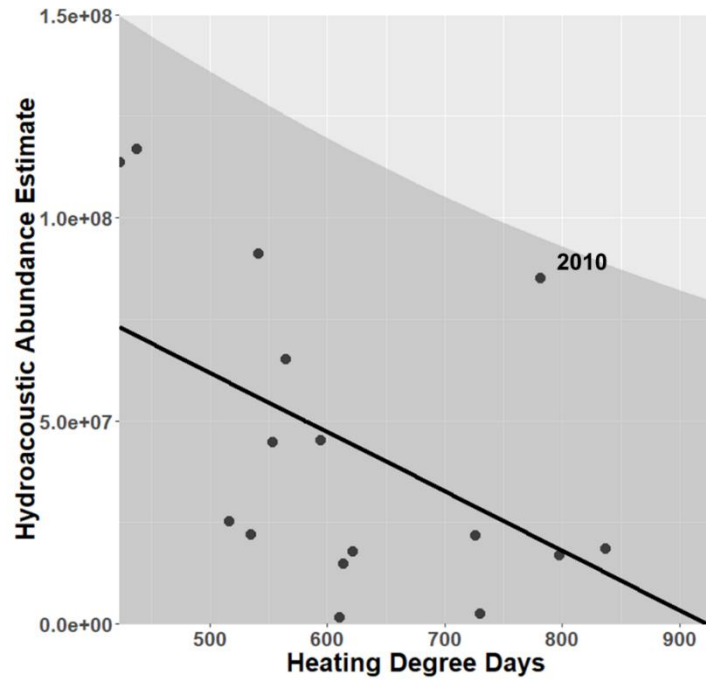


Figure 6.5: Rainbow Smelt abundance as estimated from hydroacoustics and heating degree days, 2000 – 2018, adj. $r^2 = 0.27$. Shaded area represents 95% CI.

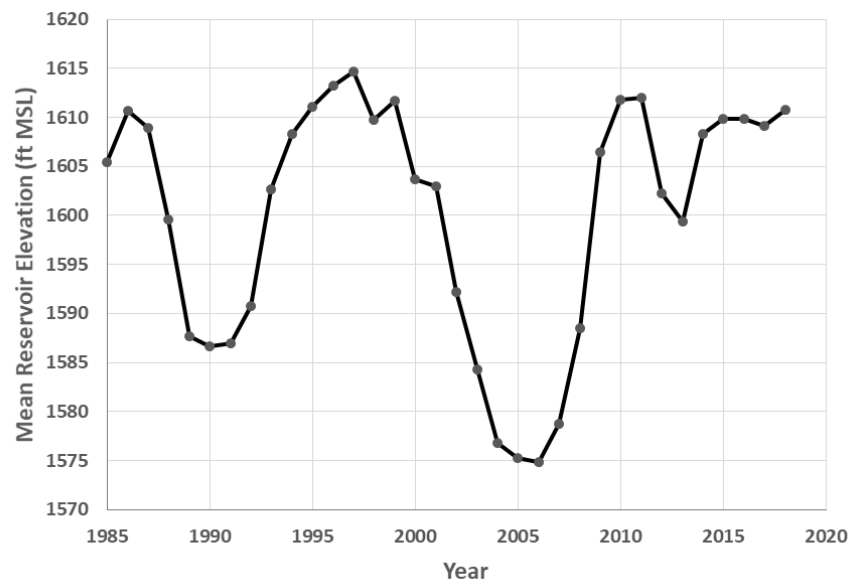


Figure 6.6: Lake Oahe annual mean annual reservoir elevation (ft MSL), 1985-2018.

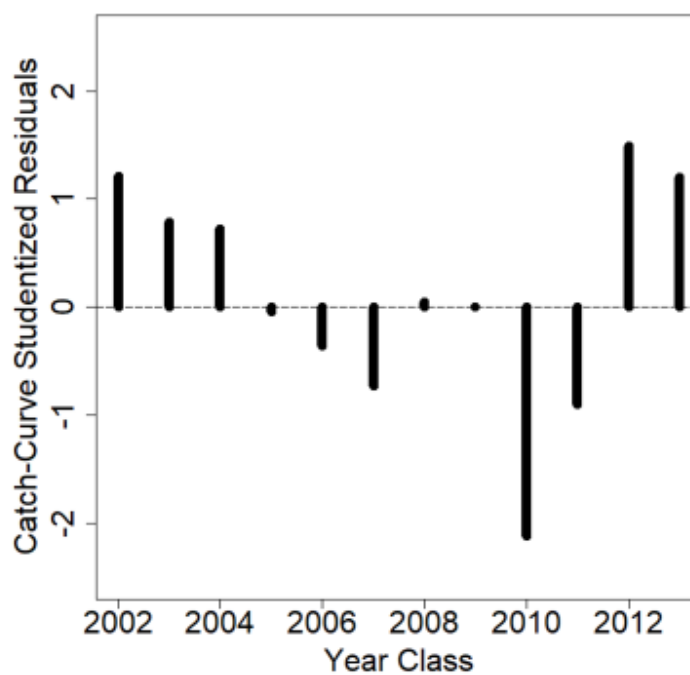


Figure 6.7: Weighted Cisco catch curve residuals. Catch curve coefficients: $F = 11.2$ on 1, 10 df , $p = 0.0074$, adj. $r^2 = 0.48$.

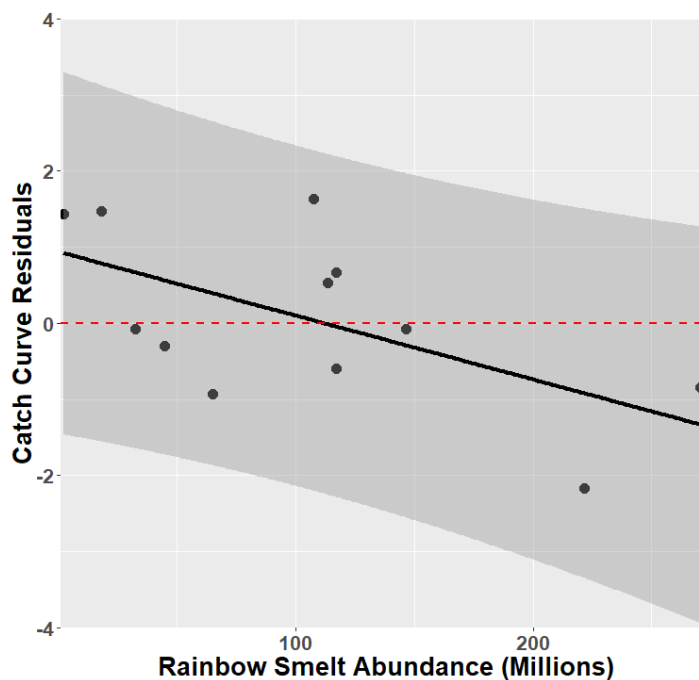


Figure 6.8: Cisco catch curve residuals and Rainbow Smelt abundance. Values near or exceeding (2, -2) are generally indicative of strong year classes, adj. $r^2 = 0.29$.

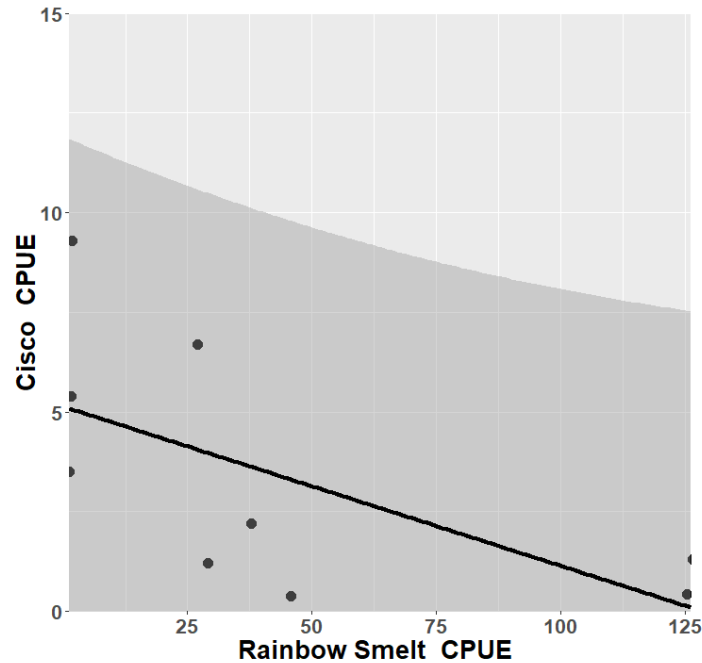


Figure 6.9: Cisco and Rainbow Smelt CPUE, cold-water suspended gillnetting 1992-2000, $\text{adj. } r^2 = 0.31$.

Table 6.1: Rainbow Smelt recruitment information theoretic multiple regression results, 1985 - 2000. Rainbow Smelt cold-water suspended gillnet CPUE was used as the response variable. Covariates were lagged 3 years, as the 3 year age class represented the annual majority of the population sampled.

	k	AICc	ΔAIC	W_{AIC}
Log ₁₀ (Reservoir Elevation)	3	22.69	0.00	0.95
Log ₁₀ (Monthly Outflow)	3	29.03	6.33	0.04
Global	7	34.39	11.70	0.00
Null	2	34.63	11.94	0.00
Heating Degree Days	3	37.51	14.82	0.00
Air Temperature	3	37.62	14.93	0.00
Precipitation	3	37.70	15.01	0.00

Table 6.2: Rainbow Smelt recruitment information theoretic multiple regression results, 2000 - 2018. Rainbow Smelt abundance as estimated from hydroacoustics was used as the response variable. Covariates were lagged 3 years, as the 3 year age class represented the annual majority of the population sampled.

	k	AICc	ΔAIC	W_{AIC}
Heating Degree Days	3	642.50	0.00	0.62
Null	2	645.85	3.35	0.12
Log ₁₀ (Reservoir Elevation)	3	646.12	3.62	0.10
Air Temperature	3	646.55	4.04	0.08
Log ₁₀ (Monthly Outflow)	3	647.93	5.43	0.04
Precipitation	3	647.94	5.43	0.04
Global	7	655.20	12.70	0.00

Table 6.3: Cisco recruitment information theoretic multiple regression results, 2002-2013. Cisco weighted catch curve residuals based on 2015 deep water gillnetting used as the response variable.

	k	AICc	ΔAIC	W_{AIC}
Rainbow Smelt (millions)	3	39.98	0.00	0.53
Null	2	41.52	1.54	0.24
Precipitation	3	44.55	4.57	0.05
Heating Degree Days	3	44.80	4.82	0.05
Air Temperature	3	44.92	4.94	0.04
Monthly Outflow	3	44.99	5.00	0.04
Reservoir Elevation	3	45.06	5.07	0.04
Global	8	91.06	51.08	0.00

Table 6.4: Cisco recruitment information theoretic multiple regression results, 1992-2000. Cisco cold-water suspended gillnet CPUE was used as the response variable.

	k	AICc	ΔAIC	W_{AIC}
Null	2	51.03	0.00	0.29
Rainbow Smelt	3	51.30	0.28	0.26
Precipitation	3	52.30	1.27	0.16
Monthly Outflow	3	52.45	1.42	0.14
Heating Degree Days	3	53.68	2.65	0.08
Reservoir Elevation	3	54.89	3.86	0.04
Air Temperature	3	55.81	4.78	0.03
Global	8	∞	∞	0.00

CHAPTER 7: CONCLUSIONS

The research presented in this dissertation covered several aspects of Lake Oahe Rainbow Smelt recruitment, monitoring, and community interactions. This information contributes to the literature addressing fisheries standard monitoring and population estimation methods. Finally, my research explored the spatial dynamics of reservoir habitat use. My work adds to the Rainbow Smelt recruitment literature (Feiner et al. 2015, Rook et al. 2013, Hoff 2004, Henderson and Nepszy 1989), and adds a novel prairie reservoir population to the literature addressing interactions of Rainbow Smelt and Cisco (Myers et al. 2009, Krueger and Hrabik 2005). Hydroacoustic monitoring of cold-water prey fishes is well-established as a method (Simmonds and MacLennan 2005), and we principally suggested a simplified interpolation and analysis method as an alternative to more intensive geostatistical approaches (e.g. Taylor et al. 2005). Finally, we added to knowledge of spatial variation in the Lake Oahe fishery, adding to the work of Felts (2018), Carlson (2017), and Fincel (2011).

Hydroacoustic monitoring of Lake Oahe cold-water prey fish utilizes a systematic transect layout ($n = 17$), and our work suggests this is a reasonable practice. From our spatial analysis of Rainbow Smelt population densities, we know the southern reaches of the reservoir generally support a lower-density population and population estimates in this zone are not improved by higher sampling effort compared to current methods. We recommend the continued use of the systematic transect layout, as we have shown similar density estimates and variance regardless of sampling intensity. A reduction in transects represents a substantial cost and effort savings for the survey. Additionally, we

recommend the more efficient longitudinal transects. These were able to deliver estimates similar to the time-intensive cross-sectional alternative. A time savings of 60.99% provides an additional savings to SDGFP. More importantly, the time savings in running the survey reduces the time biologists are performing potentially dangerous work at night. Moreover, the ability for managers to move the survey to later summer months prevents “dry-dock” nights, or periods when biologists are unable to sample due to severe weather events more commonly experienced in July and early August.

Reproduction of Lake Oahe Rainbow Smelt occurs unpredictably across the shorelines of the reservoir but is concentrated on steeper sloped habitat. Generally, these were areas not previously considered ideal spawning locations by SDGFP biologists. This is largely due to a historical gear bias, as previous understanding was based on limited mini-fyke net data (South Dakota Game, Fish, and Parks, unpublished data) that could not sample steep shorelines. In the present study, we were able to sample habitats where mini-fyke nets were not able to be fished. South Dakota Game, Fish, and Parks (SDGFP) has previously made recommendations to the U.S. Army Corps of Engineers for rising Lake Oahe reservoir elevations in the spring, and our investigations suggest this ought to be continued to limit egg stranding. Managers also wished to know if habitat enhancements on a continuing basis might bolster the unstable recruitment patterns shown over the past 40 years by Rainbow Smelt. Given the unpredictable spawning site use by adults and variable larval distribution, we believe this is not a feasible option.

The Lake Oahe fish community will continue to be impacted by Rainbow Smelt entrainment, as high spring flows have caused population crashes on multiple occasions. Recovery will likely be a function of reservoir elevation and spring weather, with recruitment favored in years with an early spring and low reservoir elevation. It is expected that Cisco will be released from predation and/or competition by Rainbow Smelt declines and produce strong year classes following declines in the Rainbow Smelt population. Historically, Gizzard Shad were the alternative prey for the Lake Oahe Walleye population during Rainbow Smelt recovery (Fincel et al. 2014). Recently, with the high recruitment of Cisco following the post-2011 flood Rainbow Smelt crash, pelagic cold-water alternative prey is present. Although we lack the data for a rigorous evaluation, it appears that the availability of Gizzard Shad and Cisco may have decoupled the Rainbow Smelt abundance – Walleye condition linkage that has been noted in multiple studies (Felts 2018, Fincel et al. 2014, Graeb et al. 2008).

Research Outcomes

Objective 1: In our comparison of two hydroacoustic survey designs and survey timing, we found 0.8 km longitudinal transects provided a time savings of 60.99% while generating similar estimates to the more time-intensive cross sectional transects. We also described hydroacoustic analysis criteria and assumption, followed by a simple interpolation method for population relative abundance estimation. Over four years, this method revealed no significant differences between survey months. Thus, we recommend the adoption of the more efficient survey and the simplified spatial analysis. SDGFP may designate a new month for the standard hydroacoustic survey

moving forward, although we recommend keeping this standardized to avoid potential temporal biases not detected in this study.

Objective 2: In our evaluation of population distribution and sampling effort for the cold-water prey base, we demonstrated inter-annual clustering of Rainbow Smelt distributions. The lower region near the dam was perennially a low density area. We determined the upper and lower zones of the stratified region of Lake Oahe could be sampled with 8 transects per zone. As this is similar to the current systematic survey effort ($n = 17$), we recommend the use of the current systematic survey, updated to the longitudinal transects as described in Chapter 1.

Objective 3: In our evaluation of Rainbow Smelt spawning ecology, we found the majority of spawning occurred between 5.8 – 6.8°C. This activity was linked to sites with steeper bathymetric slopes and deeper mean depths, and the relationship strengthened as water temperature increased. We interpret this as spawning site use relative to thermal refuge adjacency. We hoped to identify a spawning habitat niche for Rainbow Smelt that could be replicated over time around the reservoir to enhance the overall quantity of available spawning habitat, but this proved to be elusive. Habitat correlations were not detected beyond general slope and depth associations. Instead, Rainbow Smelt spawning occurs in indeterminate locations throughout the reservoir that meet general thermal criteria, attenuated by bathymetry throughout the spring warming period. As spawning was observed in shallow waters, we recommend SDGFP continue to suggest stable-to-rising spring reservoir elevations to the U.S. Army Corps of Engineers.

Objective 4: In our evaluation of Rainbow Smelt larval life history, emergence timing was highly dependent on temperature. The 3 weeks of warming, post-ice-out, to 13 – 15°C is associated with higher larval densities. In theory, if this occurs earlier in the year and temperatures are favorable, a longer growing season should lead to greater length-at-age at first overwintering. Larval growth was fastest in the southern zone, corresponding to the Bush's Landing area. There are no direct recommendations for Rainbow Smelt management from this outcome, as manipulation of lake-wide temperature regime is not realistic; however, in years with late ice-out when Rainbow Smelt recruitment is expected to be weak, SDGFP may wish to consider stocking embayments with Gizzard Shad to proactively enhance forage availability given potential future shortfalls.

Objective 5: In our analysis of Rainbow Smelt and Cisco recruitment dynamics, Rainbow Smelt recruitment was driven by reservoir elevation and spring weather, depending on temporal data range. Higher recruitment was observed at lower spring reservoir elevations, and was also associated with earlier and/or warmer spring temperatures. We predict Rainbow Smelt will continue to be impacted by entrainment, as high spring flows severely reduced the population on multiple occasions. It is expected that Cisco will be released from predation and/or competition by Rainbow Smelt declines and will produce strong year classes following a Rainbow Smelt population crash. While a short lag may occur, Cisco recruitment may provide alternative prey for the Lake Oahe Walleye population during periods of low Rainbow Smelt abundance. Recently, it appears Cisco and Gizzard Shad may have provided an adequate alternative prey base

for the Walleye population due to the increase in Walleye condition in the absence of Rainbow Smelt population recovery. We recommend the continued practice of emergency Gizzard Shad stocking when Rainbow Smelt abundance severely declines.

Research Needs

1. While Rainbow Smelt spawning site selection displays site-specific thermal and bathymetric trends, these sites have a variety of substrates and directional orientations. We anecdotally observed differential spring wave action across this habitat variety, dependent on site sheltering and orientation. Additional research to address egg and larval survival in sheltered versus exposed sites might reveal small-scale locations with young-of-year contributions disproportionate to their spatial footprint.
2. Previous otolith microchemical analysis was unable to determine reservoir-scale trends in the natal origin of Rainbow Smelt. This was primarily due to a lack of larval fish captures to establish a baseline for adult microchemical ratio comparison. We suggest revisiting this method, using our insights into larval emergence relative to spring temperature to more effectively target larval sampling. Further, our larval otolith samples were handled and stored specifically for use in microchemical research. Natal origin information would allow managers to establish linkages between the habitat patterns we demonstrated to site-specific recruitment contributions. While we demonstrated factors influencing the reproduction from spawning to the larval stage, an otolith microchemistry project would expand this to the full recruitment cycle.
3. Our research was hampered by a lack of reliable Lake Oahe water temperature data, and we were forced to use local air temperature data as a less-than-desirable proxy

variable. This issue is acknowledged in personal communication with SDGFP staff and various researchers. SDGFP may wish to establish standard temperature monitoring stations as a low-cost solution to this ongoing issue, following the Minnesota Sentinel Lakes program template. As large scale temperature changes pose a major future challenge to fisheries management, these data would have a myriad of potential uses.

4. The recent potential decoupling of Walleye growth and mortality dynamics from the unstable Rainbow Smelt prey base could be a major change in Lake Oahe system function. A timely diet study tracking Walleye resource use would provide documentation of this potential change. Given local precipitation instability is predicted by climate models, detrimental entrainment impacts on Rainbow Smelt may become more frequent in the future. Thus, it would be desirable to understand how Walleye growth and mortality will respond to a change in the Lake Oahe prey base from a Rainbow Smelt to a Cisco and Gizzard Shad dominated system.

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